QH
1
5

The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

VOL. 51 APRIL, 1954 No. 2

An Ecological Study of Invertebrates of Grassland and Deciduous Shrub Savanna in Eastern Nebraska*

UNIVERSITY OF MICHIGAN
JUN 3 - 1954
SCIENCE LIBRARY

Edson Fichter

Department of Zoology, Idaho State College, Pocatello

CONTENTS

Introduction	321	Previous faunal studies	329
Acknowledgements	322	Extent and methods of study	330
True prairie	323	Instrumentation	336
Tall-grass prairie	323	Collections	337
Postclimax deciduous shrub	324	Environmental studies	338
Background of drought	324	Population studies	347
Area studied	325	Aspection	349
Climate	325	Stratification and diurnation	371
Topography and geology	327	Accounts of prevalents	385
Soils	327	Discussion	394
Vegetation	327	Summary	406
Stations	329	References	410

Introduction

Several considerations prompt, influence, and lend significance to any serious attempt to add to or improve existing knowledge of animal populations in grassland, namely, (1) the importance of grass to the people of the Great Plains (Allred 1941, U.S.D.A. Ybk. Agric. 1948), (2) the propensities of grassed areas as sources of insect pests destructive to other crops, especially corn (Bruner 1900, Osborn 1917, 1939:16, 29, Herrick 1925:365), (3) the possible role of the ecological method of study in the control of meadow insects (Osborn 1917, 1939:10, Townsend 1924, Chapman 1939, King 1939:281, Smith 1939), (4) current operations of land and wildlife management agencies toward revegetation of exploited and submarginal lands (Robertson 1939:433, Hoover 1939, Graham 1941, Hoover *et al.* 1947), (5) the growth of the bioecological concept (Vestal 1914, Shelford and Olson 1935, Weaver and Clements 1938:478, Carpenter 1939a, and Clements and Shelford 1939), and (6) the decimation of native prairie (Adams 1915, Weaver and Clements 1938:518) accentuating (7) the need for studies on primitive or near-primitive remnants (Carpenter 1939b, Dowdy 1944a:218). The study reported here was undertaken in an effort to determine composition and behavior of the communities of invertebrates as they occurred during the period of the investigations, in a 320-acre remnant of unbroken grassland in eastern Nebraska, and in relatively small areas of two postclimaxes within the tract.

* Studies from the Department of Zoology, University of Nebraska, No. 266.

When the two-year study was initiated in 1937 it was intended that animals of true prairie were to be under investigation. It become evident, however, that under the impact of three years of drought the characteristic continuous stand of perennial, dominant mid grasses had greatly deteriorated; the more xeric dominants of mixed prairie had invaded. Rainfall patterns remained abnormal, and conspicuous and dramatic changes in the prairie continued through the two years of this endeavor. Drastically reduced plant cover, great and relatively rapid changes in floral composition, and abnormal moisture conditions may have produced invertebrate population patterns not characteristic of remnants of climax true prairie. Relative abundance of the many species of arthropods was probably altered. Osborn (1939:37) has pointed out that "a well known feature of meadow life is the varying abundance of different groups or species in different seasons or years in a series. . . ." Under the vacillating stresses present in the prairie from 1934-41, such shifts in invertebrate populations may have been magnified if not accelerated. Aberrant weather patterns may have been directly reflected in atypical behavior. Previous studies on animal communities in this or comparable tracts of true prairie in this region would have made possible comparison with pre-drought population patterns. Faunal studies should have been in progress throughout the ten-year period of great changes in the grasslands. Here was a magnificent "natural experiment" offering "a chance to deduce the response of a whole community to its weather environment" (Leopold and Jones 1947:117-118). It is regrettable that the study reported here was not continued sufficiently long to measure reliably any drought-induced changes that may have occurred in the invertebrate fauna.

The eight-year period of drought ended and recovery of true prairie vegetation began in 1941 (Weaver and Albertson 1944). Studies on animal communities of that association can again be made; they would probably add significance to much of this report.

Quantitative ecological studies of grassland invertebrates in North America are relatively few in number. King (1927) studied the fauna of native and ruderal associations at Saskatoon, Saskatchewan, with special reference to climatic influence. Prairie invertebrates have been studied quantitatively in Illinois by Shackleford (1929), with emphasis on designation of societies, and by Carpenter (1935) who made his investigations upon the prairie-forest ecotone, emphasizing fluctuations in biotic communities. Carpenter (1939b) again considered biotic fluctuations from the viewpoint of aspection in mixed prairie in Oklahoma, where he found some agreement with the conditions reported by Beed (1936) for short grass plains in Nebraska on a tract grazed only by native mammals. Shackleford and Smith (1928), Shackleford and Brown (1929), and Shackleford (1931, 1935) have studied invertebrate populations of grasslands (pastured in part) in central Oklahoma, with emphasis on seasonal and annual variations.

This paper presents results of the first quantitative ecological study of invertebrates in the true prairie, albeit disturbed by severe drought and in subsere.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge the assistance and suggestions accorded me by Dr. Irving H. Blake of the University of Nebraska, under whose direction this study has been conducted. To Dr. David D. Whitney and the Department of Zoology of the

University of Nebraska thanks are due for making possible the construction of field and laboratory equipment. I am indebted to the Nebraska Academy of Sciences for a grant-in-aid which helped defray expenses incurred in transportation and in the construction of a field laboratory. The invaluable help given me by Dr. J. H. Robertson of the University of Nevada in locating the stations is gratefully acknowledged. To Dr. J. E. Weaver of the University of Nebraska appreciation is expressed for helpful advice. For the generosity of the late Mr. T. Flader and his sons in giving me free access to the prairie tract which was under their ownership, I owe a special debt of gratitude. Thanks are due Henry Smith of the University of Nebraska who conducted the soil analyses, William McMann of the Nebraska State Agricultural Conservation Office whose cooperation made possible the inclusion of the aerial photographs, and the following entomologists for the identification of arthropods: Orlando Bare (Formicidae), H. R. Bryson and Roscoe Hill (Coleoptera), H. H. Knight (Hemiptera), Miriam A. Palmer (Aphididae), Raymond Roberts (miscellaneous insects and Ixodoidea), Curtis W. Sabrosky (Diptera), and D. A. Wilbur (Homoptera). To my wife, Ardith Fichter, whose help in organization of data and preparation of manuscript has been indispensable, I am grateful. The efforts of the following men, who as fellow students were helpful in many ways, are acknowledged with thanks: William R. Cunningham, Lloyd Don Davis, Robert Fowler, George Garrison, Merle F. Hansen, Harlan Herman, Albert Lunt, Rufus A. Lyman, Sam Messner, Robert Walstrom, and Robert Worthman.

The specimens taken in this investigation are in storage at the Department of Entomology, University of Nebraska, through the cooperation of H. Douglas Tate. I am grateful to the staff of that Department for their efforts in curating the material, for making any part of it available to other workers (see Muma and Muma, 1949), and for many other courtesies relating to this undertaking.

True Prairie

The vegetational characteristics and relationships, status, and general distribution of the climatic community which, as one of several grassland climaxes, is known as *true prairie* (*Stipa-Sporobolus* association), and of the postclimax tall-grass prairie (*Andropogon* associes) have been treated extensively by Clements, Weaver, and Hanson (1929) Weaver and Fitzpatrick (1934), and Weaver and Clements (1938). Aikman (1929) and Weaver and Clements (1938) have described the postclimax extensions of the oak-hickory association into the prairie climax along stream valleys and dry ravines. The following brief characterizations of the three vegetational complexes involved in this study are drawn from these authors.

True prairie is the characteristic climatic community of the rolling hills of the Missouri Valley within the general limits of 25 to 30 inches of rainfall. Cultivation has erased the true prairie over most of its area and its original limits have been pieced together only within the last twenty years from numerous relatively small and scattered fragments. The dominants of this association are mid grasses of both the sod and bunch life form.

True prairie is most closely related to the mixed prairie on the west and somewhat less closely to the postclimax prairie on the east; it is in contact with both and nearly enclosed by them. Several of the dominant species of true prairie are more abundant in the mixed prairie, and this is strikingly true of the relict short grasses.

Aspect societies are conspicuous and highly developed in the grassland. Four distinct aspects occur in true prairie from early spring through autumn. The number of subdominants in each aspect is usually large; the societies are, therefore, mixed and consist of several fairly abundant species.

Tall-grass Prairie

Tall-grass prairie is a postclimax to the true prairie. As the name indi-

cates, it consists of tall grasses, often six to eight feet high and belonging mainly to the sod-forming type. The societies of the postclimax prairie are essentially those of the true prairie, reenforced by additions from the deciduous forest and the meadows included in it; the number of species of composites is considerably larger.

Postclimax Deciduous Shrub

Along the Missouri River, which borders Nebraska on the east, a belt of deciduous forest varying in width from two to about ten miles forms a northwestward portion of the oak-hickory association which reaches South Dakota. Extensions of woodland, which are postclimax, border the many tributaries of the Missouri in belts fringing the bluffs, sometimes extending somewhat over the adjacent hills. The extreme outposts of the forest, although represented by relatively few species of trees and shrubs, reach far out into the prairie climax along the creeks and sheltered dry ravines which more or less dissect especially the rolling portions of the prairie. Thus the grassland is in contact over a very extensive marginal area with outposts of the forest. These long, narrow fingers of forest margin conditions reaching into the true prairie form an ecotone where grass meets deciduous woodland or shrub, in response to the operation of compensatory or protective features of topography.

Background of Drought

Weaver (1943), Weaver and Albertson (1944), and Albertson and Weaver (1945) have furnished comprehensive reports on the effects of the great drought of 1933 to 1940 on prairie vegetation, and on trees in the same region. The following account of the drought, of marked importance in this study, is taken from their papers.

That the prairie region of the Middle West was undergoing the most severe drought since the beginning of its recorded weather history was clearly evident by midsummer of 1934. The 12 months following June, 1933, was the driest weather period ever recorded for Nebraska. Rainfall in the summer of 1934 was extremely low, soil moisture became unavailable to a depth of four feet, and a terrific heat wave occurred. In 1935 it was found that losses of plant cover west of the Missouri River were heavy.

Replacement of true prairie by mixed prairie took place as a result of continued drought in an area 100 to 150 miles in width in central Kansas, eastern Nebraska, and eastern South Dakota. Studies in prairie tracts in southeastern Nebraska and northeastern Kansas showed that the formation of mixed prairie became clearly apparent in 1938, and that these grasslands were almost entirely transformed into mixed prairie by 1941.

Predrought vegetation consisted mostly of little bluestem (*Andropogon scoparius*) and big bluestem (*A. furcatus*) with only small amounts of western wheat grass (*Agropyron smithii*), side-oats grama (*Bouteloua curtipendula*), and the short grasses, blue grama (*B. gracilis*) and buffalo grass (*Buchloe dactyloides*). The chief dominant, little bluestem, mostly or entirely succumbed to drought in 1934 and 1936. Big bluestem was greatly damaged. In 1935 with approximately normal precipitation, six-weeks fescue (*Festuca octoflora*), blue grama, and especially western wheat grass, increased greatly. Certain native forbs spread rapidly, and there was invasion by many ruderal forbs. Severe drought in 1936-37 resulted in great advantage to six-weeks

fescue, blue grama, western wheat grass, and buffalo grass, with further losses of the less xeric grasses and forbs. Western wheat grass increased in amount and annual weeds were abundant.

Approximately normal precipitation in 1938 resulted in an excellent development of vegetation, thickening of cover, and production of much seed. Wheat grass, blue grama, and buffalo grass continued their spread. Big bluestem, needle grass (*Stipa spartea*), and prairie dropseed (*Sporobolus heterolepis*) thickened their relict stands and increased greatly. Ruderals and native weedy forbs decreased. Spring rainfall in 1939 was followed by severe summer drought. Wheat grass waned in competition with an enormous stand of sideoats grama. Short grasses increased; most other vegetation suffered from severe desiccation.

In the big bluestem type in ravines where *Andropogon furcatus* was the chief dominant, the total cover of grass was not significantly decreased by drought; it was merely changed in composition. The cover of tall grasses, including Indian grass (*Sorghastrum nutans*) and tall panic grass or switch grass (*Panicum virgatum*) became open, and short grasses and wheat grass became abundant in it.

Where postclimax forest extends into the semihumid and dry grassland climates, tree losses were extremely heavy during the decade of drought.

It is obvious that the findings given in this paper must be considered as reflecting composition and behavior of invertebrate populations subjected to aberrant climatic conditions in (1) grassland which was in a generally reverse though fluctuating succession from true prairie to mixed prairie—a prairie subsere induced by recurrent drought and marked by great, rapid, and complex changes in the vegetation, and (2) postclimaxes somewhat less affected by the shifting environment.

Area Studied

The prairie area here reported upon presented (1) a near-primitive and relatively large unit of the once vast true prairie, (2) a grassland area (meadow) bordered by cultivated crops (Fig. 1), and with its included postclimax areas, (3) an opportunity for comparative ecology.

The study was conducted within a continuous tract of upland prairie one-half section in extent (Lancaster County, Township 10 N.—Range 5 E., Section 2, east half), which is located five and one-half miles west and three miles north of Lincoln, Nebraska. Haying operations constituted the only important disturbance to which the vegetation had been subjected by man, with the exception of grazing by a small band of horses during one winter about 1933.

CLIMATE

Weaver and Himmel (1939) state that "the mean annual precipitation at Lincoln for a period of fifty years is 27.94 inches. Its distribution is of the Great Plains type, between 76 and 79 per cent occurring during the three months of May, June, and July. . . . Less than one-tenth of the precipitation occurs during the three winter months. The average snow fall is about 27 inches." "As a rule snow covers the ground but a few days at a time after each snow storm and the ground is covered with snow less than half of the time even during the months of heaviest snow fall" (Loveland 1920).

The mean annual temperature is 53°F. in southeastern Nebraska. January

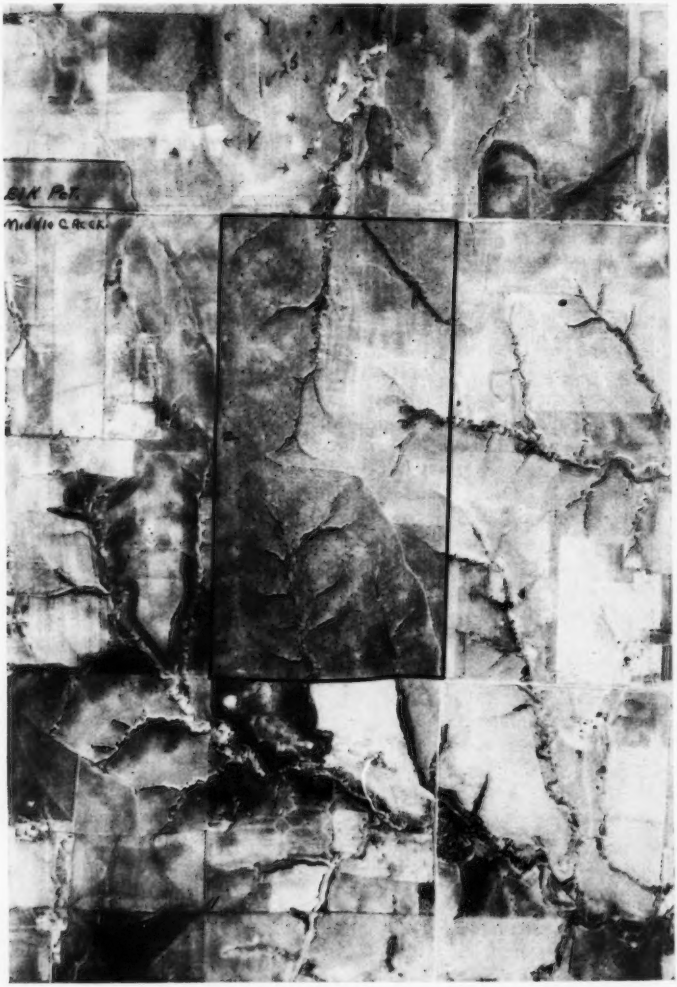


Fig. 1.—Aerial view of the half-section tract of unbroken grassland (outlined) and the adjacent areas of cultivated lands.

is the coldest month with a mean temperature of about 23°, July the warmest, with a mean temperature of about 76°. "Maximum temperatures from 96° to 100° usually occur a few times during the warm season, July, August, and the first ten days of September, and temperatures of 110° to 114° have occurred, but they are unusual. Minimum temperatures 15° to 20° below

zero occur at intervals during the cold season, the latter part of December, January, and February. Occasionally temperatures 10° lower occur.

"The prevailing direction of wind for the year is from the northwest unless influenced by local conditions. The wind blows from the south or southeast the greater portion of the time during the warm months of June, July, and August, and of course with greater or less frequency during the rest of the year. From the middle of September to the middle of May the prevailing direction of the wind is from the northwest.

"The velocity of the wind has been recorded carefully at only one station in the territory—Lincoln. The anemometer is placed at an elevation of 84 feet and the average velocity is 11 miles per hour.

"The average relative humidity for the year is quite regularly near 70 per cent. It is frequently low during the afternoon in spring or summer, sometimes below 20 per cent.

"The sky is relatively free of clouds; 175 to 185 clear days may be expected, from 81 to 86 cloudy, and the rest of the days of the year will be partly cloudy" (Loveland 1920).

TOPOGRAPHY AND GEOLOGY

The tract is dissected by five major ravines, two draining to the north, two to the south, and one to the east (Figs. 1, 2). The highest of the rolling, flat-topped drift hills is approximately 140 feet above the lowest point. Topographic maps show the 1300 foot interval line traversing the tract. The ravines are of moderate depth, showing no erosion.

SOILS

The soil is Carrington silt loam of glacial origin. Steiger (1930) and Robertson (1939) have pointed out the high water holding capacity of the soil due to the large proportion of very fine sand, silt, and clay. Robertson states that the soil is "dark, granular, friable, and without lime in the first foot but harder, yellow, and speckled with grains of lime at a depth of three feet."

Table 15 represents a summary of data for soil samples taken in the three stations on March 23, 1942. It is notable that percentages of organic matter, volatile matter, nitrogen, and hygroscopic coefficient each show consistent gradients, with the highest values occurring in the shrub station, the lowest in the subseral true prairie station. Hydrogen-ion concentrations likewise conform to a consistent gradient, soil from the true prairie station being most acid, though only slightly so (6.4), that from the shrub station the least acid (6.8).

VEGETATION

In the years 1927 and 1928 Steiger (1930) intensively studied the structure of the prairie vegetation found upon the tract wherein this investigation was conducted. Robertson (1939) reported upon the vegetation of this half-section as he found it during the summers of 1936 and 1937. The following description of the area before and after drought is based largely upon their accounts.

Steiger described what he termed low prairie occupying a broad, nearly level expanse at the foot of a north slope and at that time (1927-28) characterized by a continuous, dense sod, predominantly composed of big bluestem,

with the upland or high prairie characterized by more open ground and a varied pattern of little bluestem, needle grass, June grass, dropseeds, grama grass, and a profuse growth of non-grassy subdominants. Robertson states that before the drought the most abundant forbs, in order of decreasing importance, were lead plant (*Amorpha canescens*), prairie cat's-foot (*Antennaria campestris*), goldenrod (*Solidago glaberrima*), and the many-flowered psoralea or wild alfalfa (*Psoralea floribunda*); the many-flowered aster (*Aster multiflorus*) ranked eighth in 1928.

The vegetation of the ravines or draws is more mesic than that of low prairie, the flora varying greatly with depth of the ravines and their exposure to insolation and wind. Trees and shrubs may extend to the heads of ravines on north slopes; in the south-facing slopes trees and shrubs occupy only the lower portion. Boxelder (*Acer negundo*), western cottonwood (*Populus sargentii*), and three species of willows (*Salix cordata, S. amygdaloides,* and *S. nigra*) are the only trees. They are all of relatively small stature and occur in small groups or, more usually, as isolated individuals. Small thickets and scattered clumps of shrubs accompany the trees, often extending farther up the ravines; some of the shrubs, especially poison ivy (*Rhus toxicodendron*) and smooth sumac (*Rhus glabra*), extend into the low prairie. Wild plum (*Prunus americana*), dogwood (*Cornus stolonifera*), elder (*Sambucus canadensis*), sandbar willow (*Salix interior*), and buckbrush (*Symphoricarpos occidentalis*) also occur. Prairie grasses tend to be absent in the partial shade under the woody species where a few mesic woodland herbs, such as bedstraw (*Galium* sp.), find suitable habitat, although frequently the ground layer consists mostly of bluegrass (*Poa pratensis*). The transition from shrubs to grassland is abrupt and follows the line determined by the annual mowing. The more xeric vegetation of the steep banks, where run-off is high, is in striking contrast to that of the moist bottom of the ravine (Fig. 8).

In late July and early August of 1936, during extreme drought, Robertson found that the more mesic grasses of this prairie area were so brittle that stems readily broke off underfoot. Many large cracks were present, especially in bluegrass sod. The most abundant grasses were big bluestem, little bluestem, and prairie dropseed. The last appeared to have come through the drought of 1934 nearly unscathed. Needle grass and side-oats grama were common and of general distribution.

Only the most deeply rooted upland forbs, for example *Amorpha* and *Aster,* were not badly dried. *Aster* had advanced from eighth position to replace *Amorpha* as the most important forb.

In 1937 certain vegetational changes were obvious owing to the drought of the previous year. Much prairie dropseed and bluegrass had been killed, leaving numerous areas protected from erosion only by dead crowns and rhizomes. These and other areas were rapidly being invaded by western wheat grass and *Aster,* in some instances nearly to the bottoms of ravines. The rank growth of *Aster* and other weedy species, coupled with the sparseness of perennial grasses, reduced the value of the hay so that most of the prairie was left unmowed. The loss of bluegrass was due in part to severe injury by grasshoppers. Other perennial grasses which lost ground were side-oats grama, June grass, and the carices. Needle grass and switch grass showed small gains, but wheat grass increased over 40 per cent. Comparable increases were shown

by aster, daisy fleabane (*Erigeron ramosus*), and peppergrass (*Lepidium* sp.) —these three species being representative of perennial forbs, annual forbs, and ruderals. Perennial grasses alone were reduced by the drought.

The south half of the prairie tract was burned by the owners on April 11, 1938. By April 18 much of the burned appearance had been lost due to the rapid growth of the grasses. During the week of May 2-9 many forbs were blooming. By June 17 the picture was dominated by daisy fleabane which was in flower, and by alternes of western wheatgrass. On July 18 it was apparent that the grassland was beginning to lose its green color, due mostly to the browning of needlegrass. The bluestems were putting up flowering stalks, goldenrod was in bloom, with the daisy fleabane noticeably on the decline, the area no longer whitened by its flowers. The prairie was very dry by August 13, leaves of the grasses tightly rolled much of the time, with the general appearance brown except on north slopes and in ravines. The leaves were falling from the wild plum and dogwood in the ravines. Mowing of the prairie hay was begun on August 13 in 1938, hay from most of the north half being in stacks by August 22. Mowing in 1939 did not begin until about September 1.

THE STATIONS

The location of Station 1 (Figs. 2, 5) was chosen after careful scrutiny of the entire half-section in an effort to determine what appeared to be average conditions of slope, exposure, and floristic structure. This station was placed slightly below the rounded top of the next to highest hill of the tract, on a south-southeast slope (high prairie of Steiger 1934). Needlegrass, side oats grama, little bluestem, June grass, and dropseed were the most abundant grasses. Much bare soil surface was evident with little or no litter. The many-flowered psoralea was the most prominent forb. *Erigeron* was markedly abundant in the true prairie subsere substations.

Conditions of tall-grass postclimax considered to be typical for the area were found in a ravine which was centrally located in the tract and which drained to the south-southwest. Station 2 (Figs. 2, 6) was established here, where big bluestem, wild rye (*Elymus canadensis*), switch grass, and bluegrass characterized the vegetation, forming a dense sod, with the many-flowered aster the prominent forb.

Station 3 (Figs. 2, 7, 8, 9) was located near the northeast corner of the tract. Here an area some 20 yards long and about 15 yards wide was rather densely covered by dogwood, wild plum, smooth sumac, buckbrush, and wild grape (*Vitis* sp.).

Substations for the purpose of quantitative sampling were established within the 320 acre tract, five in the true prairie subsere, one in the ravine postclimax tall grass, and two in the ravine postclimax shrub.

Station 1, equipped with meteorological instruments, was put in operation on November 2, 1937, and Stations 2 and 3 on January 4, 1938. Collecting was begun in all three stations on November 2, 1937.

PREVIOUS FAUNAL STUDIES

Whelan has published briefly annotated lists of the Coleoptera (1936a), the Orthoptera (1938), the mammals (1936b), and the birds (1940) of this prairie tract.

Fig. 2.—Aerial view of the half-section tract of subseral true prairie and the included postclimax habitats occupying ravine situations, showing location of stations. 1. Upland true prairie subsere station. 2. Postclimax tall-grass station. 3. Postclimax deciduous shrub station.

Extent and Methods of Study

In this paper the attempt is made to point out some of the measurable factors of the physical environment and the composition of the invertebrate

communities in upland true prairie (in drought-induced subsere), and in postclimax tall grass and postclimax deciduous shrub with both of which the true prairie is in contact. Attention is focused upon (1) the differences of the environmental complexes within the three habitats studied, (2) the faunal interrelationships of these three stations, (3) horizontal and vertical movements as exhibited by stratal, seasonal, and daily total population trends, and (4) the strato-seasonal activities of prevalent species with the view of determining any indicator values (Fichter 1939:211, King 1939:281) such numerically prominent species may possess. "In making quantitative sample collections . . . the quality of the work can be greatly improved by seeking out the species occurring in any abundance" and observing their role in the community (Shelford 1930).

No effort is made to estimate the areal numbers of invertebrates. Population trends are sought, and these are considered determinable by comparison of unit collections, especially where it is possible to secure enough samples within a given stratum of a given station to allow for the determination of sample averages within a given season or other unit period. I am in accord

Fig. 3.—General view of the prairie tract, looking southeast from near Station 1, showing postclimax vegetation in ravines and the field laboratory.

Fig. 4.—Field laboratory on the prairie. The construction of this unit was made possible through a grant-in-aid from the Nebraska Academy of Sciences.

with Beall (1935) who writes that "a more legitimate use for the sweep collections of insects and arachnids, than the estimate of numbers per unit area, is to compare those made at different times and to determine population trends."

Park (1939) in emphasizing the desirability of the acquisition of more basic facts about population trends in the field, says that "both the single-

Fig. 5.—Upland true prairie subsere station during late estival aspect, 1938.

Fig. 6.—Postclimax tall-grass station, late estival aspect, 1938.

species population and the mixed-species population possess a structural or quantitative aspect which . . . merits our attention and analysis."

The desirability of designating an animal species which is abundant in its given community by the term *prevalent*, in preference to the word predominant

Fig. 7.—Postclimax deciduous shrub station, estival aspect, 1938.

Fig. 8.—Interior of postclimax deciduous shrub station, estival aspect, 1938.

as suggested by Shelford (1926) "as covering all organisms of outstanding abundance or obvious importance," has been pointed out (Fichter 1939). Prevalent species are determined on the basis of strato-seasonal abundance, i.e., that species which shows the highest seasonal population within a given stratum thereby attains prevalent rank for that season, a designation which indicates only that the species has prevailed numerically in that stratum. Such a determination of prevalents, as carried out in this study, does not purport to lend basis to the naming of societies.

Shelford (1932:107) has proposed "the importance of the abundant or otherwise significant species" in the classification of communities, and the value of characteristic though less abundant species as indicators. I am in accord with the principles of ecological classification stated by Shelford (1932:107-108), and with his suggestion that "a definite assemblage of organisms" can be relied upon as a safe criterion in the classification of communities, but I cannot subscribe to such nomenclatural appointments founded on short-time studies, especially on remnant areas. It is improbable that the existence and nature of any "definite assemblage" of terrestrial organisms can be reliably determined within the period of time given to any ecological study made to date. Osborn (1939:25) has pointed out that quantitative determinations on insects of grasslands "in any one place or for any one season cannot be assumed to represent the general [characteristic] condition . . . even for meadows of different history in the same locality." Blake (1931:524) has shown that species of animals, on which have been based application of detailed nomenclature to terrestrial animal communities, "may fail to appear in important numbers and relations in" similar studies "made on the same ground at a different time."

A species which exhibits a seasonal population less than that of the prevalent, and which may or may not equal the frequency values of the prevalent, but which exceeds the population values of the latter at one or more brief intervals, even in any one sample collection, is considered as possessing *sub-*

Fig. 9.—Postclimax deciduous shrub station, hiemal aspect, 1938-39.

prevalent rank. All prevalent and subprevalent species among the invertebrates as determined by this study are reported in this paper, with special reference to the prevalents. A few characteristic and conspicuous forms which did not attain prevalent or subprevalent rank are considered.

Four strata were studied in the true prairie subsere and postclimax tallgrass stations; namely (1) soil, (2) litter, (3) soil surface, and (4) herb, with the addition of (5) the shrub stratum in the postclimax deciduous shrub station. The soil stratum was sampled to a depth of four inches (10 cm.), always beneath the one square foot of litter collected for examination from the litter stratum. The soil surface invertebrate fauna was studied by use of an alcohol pitfall, designed to trap "those species which travel, for the most part, over the surface of the ground, and, though closely associated with the litter as material for abode, constitute when active (not resting, hiding, or hibernating), a distinct society" (Fichter 1941). This apparatus does not measure any given unit of soil surface population at any given time but does appear to indicate population trends. The population of the herb and shrub strata were sampled by the sweep net method of previous workers at 0-75 cm. in the herb and 1-2 meters in the shrub.

While the litter stratum in the shrub station approaches the condition found in climax deciduous forest, and should perhaps be more properly designated as litter-duff, the term litter will be retained here.

Field operations began on November 2, 1937, and terminated on November 4, 1939. The seasonal studies (sweeps, and litter and soil sampling) were carried on from November 2, 1937 to March 20, 1939, the day-night studies (sweeps only) from June 12 to October 29, 1938, and the pitfall studies from April 8 to November 4, 1939. A total of 187 unit day sweep collections in the herb stratum of the three stations yielded 44,418 specimens, while 2,782 specimens were taken in 24 unit sweep collections in the shrub stratum. Night sweep collections numbering 52 in herb and shrub strata collected 17,779 specimens. Soil collections numbered 63, producing 689 specimens, litter samples 102 with 4,982 specimens, and 76 pitfall collections secured 11,161 specimens. This study is thereby based upon the examination of 81,811 specimens of invertebrates taken in 504 collections.

From June 17 to August 15, 1938 I maintained a field laboratory and living quarters on the prairie tract (Figs. 3, 4). This floored and screened tent made it possible to take samples with greater regularity and to care adequately for large numbers of specimens. An average of five days and nights out of each week were spent on the area during this two-month period.

The term invertebrate as herein employed includes only the phyla Annelida and Mollusca and the classes Arachnida and Insecta; although members of the orders Acarina (mites), Collembola (springtails), Thysanoptera (thrips), and Corrodentia (psocids and book-lice) were taken they are not included in this study. It must be stated, however, that the importance of these latter groups, particularly of the mites and springtails, is thoroughly recognized.

The inclusion of small, postclimax areas in an ecological study of true prairie animals seemed advisable because of the juxtaposition of these vegetational units and the more or less universal occurrence of such postclimax vegetation throughout the prairie formation (Weaver and Clements 1938:85). These more or less distinct local habitats are expressions of immediate physi-

ographic features and each presents an ecologic problem of its own (Osborn 1939:16).

The seasons as delimited in this paper are based upon the vegetational aspects of the prairie outlined by Weaver and Fitzpatrick (1934). The prevernal and vernal are combined to form the prevernal-vernal, and the serotinal of Weese (1924) and others is included in the autumnal.

The time basis, other than the natural aspectional divisions, employed in this paper for the expression of data is the two-week period. Three short periods appear in the tabulations: a seven-day period of December 14-21, 1937, a period of thirteen days from January 18-31, 1938, and one of twelve days from September 12-24, 1938. The transition from one aspect to another is, of course, a gradual one. To facilitate seasonal study of collections made in the prairie tract it was necessary, however, to define aspectional limits. The following dates were established to keep intact the two-week periods which occurred at these transitional periods and at the same time conform closely to the normal aspect limits given by Weaver and Fitzpatrick (1934): Hiemal, November 2, 1937 to March 28, 1938; Prevernal-vernal, March 28 to May 23, 1938; Estival, May 23 to August 1, 1938; Autumnal, August 1 to October 22, 1938; Hiemal, October 22, 1938 to March 25, 1939; Prevernal-vernal, March 25 to May 20, 1939; Estival, May 20 to July 29, 1939; Autumnal, July 29 to October 22, 1939; and early Hiemal, October 22 to November 4, 1939.

This population study is neither comprehensive nor exhaustive. The lack of correlated laboratory experimentation (King 1939:284) is an admitted weakness. Relatively few conclusions can be drawn from these findings. They are offered, however, as the results of a further effort in the vast amount of work known to "be necessary before valid generalizations can be drawn" regarding terrestrial invertebrate populations — generalizations which, it is hoped, will "in turn serve as valuable guides to both economic and general work" (King 1939:281). Most of the data gathered are presented in order that workers less "handicapped by unwillingness or inability to correlate and fully utilize the data secured" (King 1939:284) may have access to them.

INSTRUMENTATION

The environmental factors, soil temperature, air temperature, relative humidity, wind, and evaporation stress were studied in each of the three stations. Precipitation was measured in a rain gauge at the true prairie station (Station 1). Light intensity (Table 14) was measured in foot candles at the surface of the soil in each station. This admittedly inadequate information on light was secured on July 1, 1938 between 11:30 A.M. and 12:30 P.M., at which time the sky was entirely clear; readings were taken with a Weston photometer at intervals of 1 meter over a 9 meter random transect in each station. Hygrothermographs were in operation in Stations 1 and 3 from the time these stations were established until the end of the period of study, and in Station 2 from August 12 to November 4, 1939. Station 3 was equipped with a soil-air thermograph from January 4, 1938 to April 29, 1939. Only air temperature was recorded in Station 2 from April 29 to August 12, 1939. Soil temperature was recorded by soil thermograph in Station 1 from November 2, 1937 to November 5, 1938 and in Station 3 from January 4, 1937 to February 11, 1938. Three-cup anemometers recorded total miles of

wind in Stations 1 and 3, while Station 2 was equipped with a four-cup anemometer.

Livingston cylindrical porous cup atmometers with non-absorbing mountings were operated in duplicate in all stations from June 20 to September 12, 1938. These atmometers were so placed in the herb stratum that the evaporating surface fell between 30 and 40 cms. above the soil surface, a level approximating one-half the height of the herb stratum, and the level through which passed the greater portion of the arc of the sweep net stroke; those in the shrub stratum of Station 3 were placed two meters above the ground. Anemometers were mounted with their cups at ½ meter above the surface of the ground, the hygrothermographs with their sensitive units at approximately 10 cm., and the soil thermograph sensitive units at 10 cm. beneath the soil surface. All of the recording instruments were housed in screened and ventilated wooden shelters.

It is to be noted that the inherent difficulties incurred by the use of instruments was apparently somewhat aggravated in the present instance by frequency of dust storms during the study. Such atmospheric conditions, while not particularly severe at any time, and often of local nature, made it impossible to keep recording instruments as free of disturbing elements as desired. It is my opinion that further inaccuracies in recorded meteorological data are introduced by the use of green shelterhouses; while green offers a desirable camouflage, shelters painted this color tend to absorb radiant energy, and, in spite of apparently adequate ventilation, thereby alter the conditions of temperature (and possibly relative humidity) to which the instrument is exposed, with respect to those in the surrounding vegetation. It is suggested that recording instruments in all studies in the field be housed in shelters painted *white* and equipped with a *double roof*.

Further difficulties were caused by crickets and spiders finding their way into certain of the shelters. Hygrothermograph hairs were eaten by crickets in two instances. The spiders spun webs in the sensitive units.

Drifting snow often completely filled the shelterhouses and covered wind gauges.

COLLECTIONS

The sweep net method of quantitative sampling was employed in the herb and shrub strata. Fifty uniform strokes of a sweep net measuring 30 cm. in circumference, with a 35 cm. handle, constituted a unit sweep collection at 0-75 cm. above the surface of the ground in the herb stratum of the true prairie subsere and tall grass stations. In the shrub station the average single stroke of the sweep net in the herb stratum was of necessity about two-thirds that in the more open vegetation; seventy-five strokes, therefore, formed a unit sweep collection here at 0-75 cm. above the surface of the ground. Ten strokes were taken as a unit collection at the 1-2 meter level in the shrub stratum, and these on the periphery of the shrubs. Invertebrate population values obtained in the shrub stratum were mutliplied by five to allow comparison with samples from the herb stratum. The impossibility of accurately establishing and maintaining a standard stroke of the sweep net in different types of vegetational complexes demands that the investigator must admit the probability of discrepancies in his findings. These inherent difficulties make desirable the securing

of large numbers of samples. The fluctuations which invertebrate populations exhibit may, thereby, be more exactly traced.

Litter samples were taken with the enclosed quadrat, a 12x12 inch sheet iron box, open at the bottom, and equipped with a handle and a corked aperture on the closed top. After the instrument is placed quickly over the spot to be sampled, the edges are forced into the soil an inch or so. Ether is introduced through the hole in the top, which is then corked. After the litter inhabitants are sufficiently anesthetized, the litter is gathered by hand into a paper sack and removed to the laboratory for examination. The soil beneath the now bared area is removed to a depth of 4 inches (10 cm.) and placed in tin pails for transportation. In this study the soil was treated with sodium bicarbonate (1 heaping tablespoonful to 1 gallon of water) for 4 to 6 hours to partially break down the flocculation. Then it was put through a soil washer (Shelford 1929), an apparatus which is effective in securing only the larger forms in the soil, its successive screens measuring 2, 4, 8, and 16 meshes to the linear inch.

The square foot sample from the litter stratum, even when "used to an extent within the limitations of a single investigator" does not furnish desired information on species that may be noted as abundant on the surface of the soil (Fichter 1941). That the square foot sample appeared to fall below the minimal area requirements for the quantitative study of soil surface forms in spruce-fir forest has also been noted (Blake 1945). The alcohol pitfall, previously referred to as designed for the comparative study of the wandering, relatively swiftly moving, ground surface arthropod populations, secured continuous collections in each of the three stations while in use.

Environmental Studies

Precipitation records taken in Station 1 (Table 1) show a yearly total (March 28, 1938 to March 25, 1939) of 32.37 inches, 4.43 inches above the mean annual value of 27.94 given by Loveland (1920). The total rainfall figures for the estival periods of 1938 and 1939 are 8.71 and 8.82 inches, respectively. The prevernal seasons of the two years are at considerable variance, however, 8.64 inches of rain being recorded in that season of 1938, and only 2.9 inches in 1939 (Figs. 10, 12).

It is felt that precipitation values secured in this station during the winter months may have been somewhat high due to inaccuracies introduced by melting snow.

Air temperatures (Tables 2, 3, 4) during the period of the study appear to have maintained approximately normal values. The mean temperature in Station 1, as calculated from thermograph records, was 54.2°F., 1.2° in excess of the mean annual level of 53.0° for southeastern Nebraska. Means determined for the postclimax tall-grass and deciduous shrub stations still more closely approached the fifty year mean, being 53.5° and 53.6° respectively (Table 16).

The maximum air temperature value for the period, 112°F., was recorded by the thermograph in Station 1 as occurring during the two-week period ending August 15, 1938 (Table 2). As previously stated, it is possible that temperatures higher than the true air temperature may at times occur inside the instrument shelters. The lowest air temperature recorded during the study was –22.0°F., this level being reached in the tall grass station (2) during the

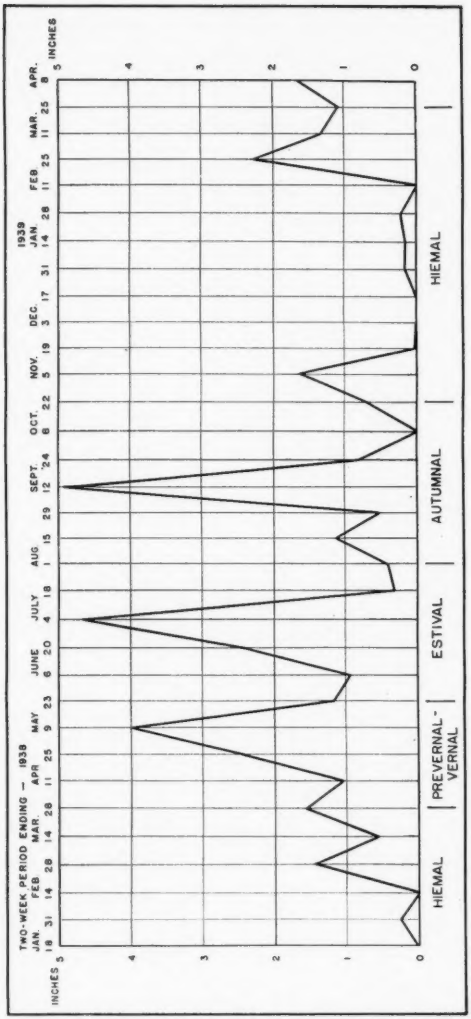


Fig. 10.—Amount of precipitation recorded by rain gauge in the prairie tract (Station 1), January 4, 1938 to April 8, 1939, expressed as total inches per two-week period.

two-week period ending January 31, 1938 (Table 3). The lowest fortnightly mean minimum and lowest fortnightly mean air temperature values, 16.4° and 19.0° respectively, also occurred in Station 2 during the two-week period ending February 25, 1939 (Table 3). The corresponding two-week period of the preceding year, that ending February 28, 1938, shows the fortnightly mean air temperature of 29.5° as the low for that winter (Fig. 11).

A single marked annual peak of fortnightly mean air temperature occurred

early in the autumnal season of 1938, the two-week period ending August 15 producing a high mean of 83.7°F. in the true prairie subsere station (Fig. 11). A lesser though well defined temperature peak is shown for the same season, produced eight weeks later by the mean for the two-week period ending October 8. In 1939 an estival temperature peak constituted the annual peak, as

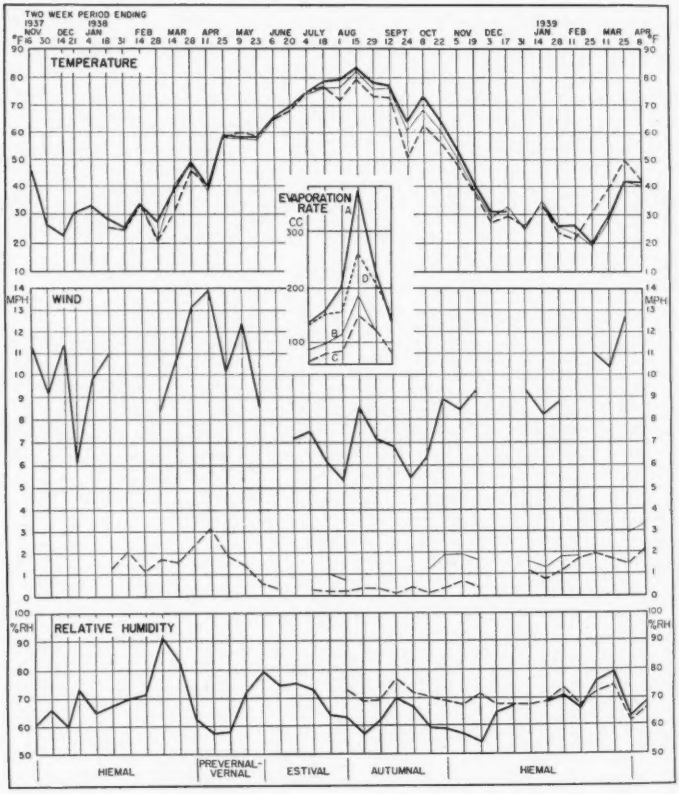


Fig. 11.—Physical factors of the atmosphere, November 2, 1937 to April 8, 1939. Discontinuous lines indicate mechanical failure of recording apparatus. *Temperature* (mean °F. per two-week period, in the herb stratum): Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line). *Evaporation rate* (loss in cubic centimeters from standardized atmometers per two-week period, June 20 to September 12, 1938): Subseral true prairie, herb stratum (line A); Postclimax tall grass, herb stratum (line B); Postclimax deciduous shrub: Herb stratum (line C); Shrub stratum (line D). *Wind* (mean MPH per two-week period at 0.5 meter): Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line). *Relative humidity* (mean per cent per two-week period in herb stratum): Subseral true prairie (solid line); Postclimax deciduous shrub (broken line).

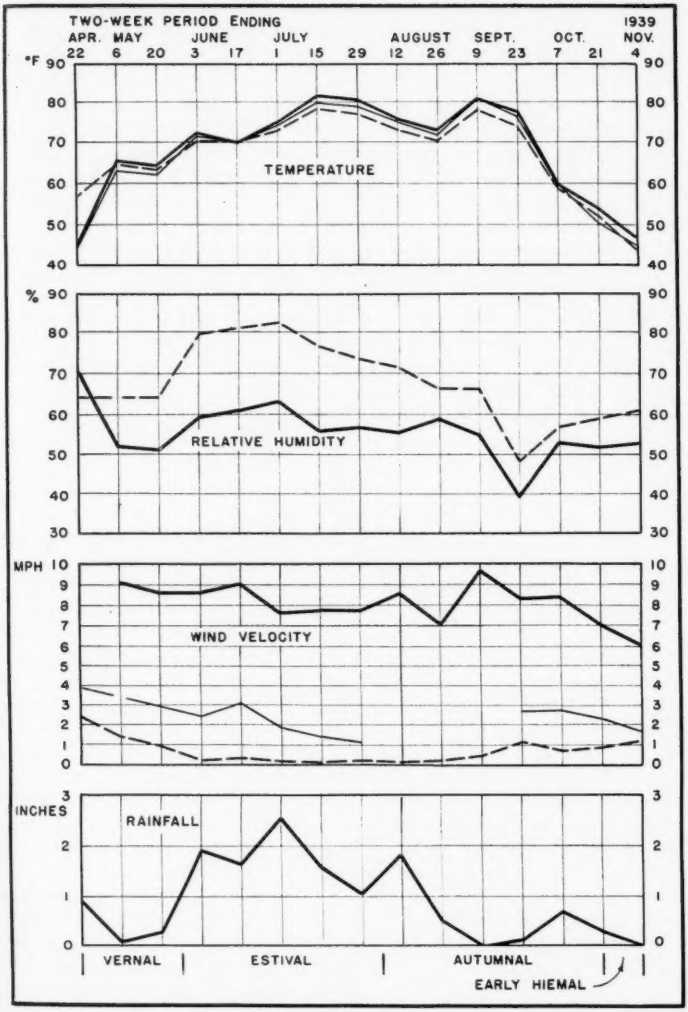


Fig. 12.—Physical factors of the atmosphere, April 8 to November 4, 1939. Discontinuous or omitted records indicate mechanical failures of recording apparatus. *Temperature, relative humidity, and wind velocity:* Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line, omitted in relative humidity graph); Postclimax deciduous shrub (broken line). *Rainfall:* Includes all precipitation as measured by rain gauge in the subseral true prairie station.

based on averages for two-week periods, coming a month earlier than the 1938 peak (Fig. 12). It is of special interest to note that in this second year of study a second fortnightly mean temperature peak again occurred, and again followed the major peak by eight weeks; in this instance, however, the second peak was of nearly the same magnitude as the first.

The mean relative humidity for Stations 1 and 3 as calculated from hygrograph records (Tables 5, 7) was 64.1% and 69.3%, respectively, (Table 16), the latter more closely approaching the "near 70 per cent" annual value previously quoted from Loveland (1920). Periodic means of relative humidity, of two-week intervals in this instance, usually showed slight though irregular variations from a comparatively uniform annual level. Records from this study (Station 1) show, however, a definite high for the two-week period ending February 28, 1938 followed by consistently decreasing values and a distinct low with means of 57.7% and 58.1% for the two-week periods ending April 11 and 25, respectively. This low is in turn followed by a definitely constant increase to a lesser peak of 75.3% for the two-week period ending June 20. While the curves of relative humidity show, for the most part, vacillations which in some cases are apparently not correlated with temperature differences, a condition reported by Blake (1926:47[411]) for pine-hemlock forest in Maine, it seems significant here that the one marked high of relative humidity is coincident with the 1938 low of temperature already noted, although they occurred in different stations (Fig. 11).

Also noteworthy are the concurrent fall in relative humidity and sharp rise in temperature in the spring of 1939; a marked autumnal low of relative humidity lags somewhat behind the autumnal air temperature peak (Fig. 12).

The annual mean wind velocity of 8.82 MPH for the upland true prairie subsere station was 2.18 below the Weather Bureau mean of 11.0 MPH for the Lincoln area. This variance is possibly accounted for by the differences in placement of anemometers relative to the surface of the earth and to vegetation. The anemometer in the subseral prairie station, being near the top of a hill and in comparatively low vegetation (drought-stricken grasses), was in a relatively exposed situation. The record from this instrument would thereby be expected to approach that of the Weather Bureau anemometer, about seven miles separating the two stations. Wind velocity was greatest during the latter half of March and the first half of April, a fortnightly mean of 13.92 MPH recorded between March 28 and April 11, 1938, in Station 1 forming the peak. The two-week period showing the lowest mean wind velocity in Station 1 is that ending August 1, 1938 (Table 8). The following fortnight produced an early autumnal peak, of considerably less magnitude than the prevernal-vernal high, but well defined and coincident with the high in air temperature for that year (Fig. 11). Similarly, an autumnal peak of mean wind velocity coincides with the autumnal air temperature peak of 1939 already discussed (Fig. 12).

Soil temperatures (fortnightly means, Tables 10, 11, 12; Fig. 14) show the usual lag behind air temperatures in the attainment and relative constancy of the hiemal low and the late-hiemal upturn in March of 1939. Those for the winter of 1937-38, however, show the late-hiemal rise beginning in mid-February, roughly a month earlier than in the following year. This suggests relatively higher insolation values in the winter of 1937-38 and the production

of soil temperatures which show little or no lag behind air temperatures. This condition may have been a correlative of the "general recovery" of vegetation, "thickening of cover," and "decrease in amount of bare soil" reported for the growing season of 1938 by Weaver and Albertson (1944:403).

The lowest soil temperature that occurred during the period of the study was recorded in Station 1, when the 22.5°F. level was reached during the fortnight ending February 14, 1938. Station 1 also produced the maximum soil temperature during the study, a value of 90.0°F. This peak occurred in the two-week period ending August 29, 1938, exhibiting the usual lag behind air temperature, the 1938 peak of which was attained in the two-week interval preceding, i.e., ending August 15 (Fig. 11).

Of more interest in this problem than the general weather picture is the comparison of climatic factors in the three biotic communities investigated. Pertinent comparative data are summarized in Table 16 on the basis of seasons. The aerial factors of air temperature, wind velocity, evaporation rate, and relative humidity as determined in the three stations during the period of the seasonal and day-night studies (November 4, 1937 to April 8, 1939) are graphically presented in Fig. 11, and the factors of precipitation, soil moisture, and soil temperature for the same period in Figs. 10, 13 and 14, respectively. Comparative values of air temperature, relative humidity, rainfall, and wind velocity in the three stations during the period of the pitfall studies (April 8 to November 4, 1939) are given in Figure 12.

It will be noted that slight differences in seasonal means of air temperature occurred in the three stations, the autumnal means of Stations 1 and 3 showing the greatest seasonal variance, 3.3°F., the hiemal means of the three stations falling within the seasonal minimum range of 1.2°F. Perhaps of greater significance are the differences in seasonal mean ranges of air temperatures that occurred in these three situations. Here the greatest variance is shown in the prevernal-vernal season, the postclimax deciduous shrub station producing a mean range of 7.6° in excess of that in the subseral true prairie, while in the postclimax tall-grass station the annual mean range is 9.4° over that in the true prairie subsere station. Seasonal means of air temperature in the shrub station are somewhat below those in the other two stations in the estival and autumnal periods, slightly above the mean in the tall-grass station in the hiemal, but notably above the other two stations in the prevernal-vernal. Figures 11 and 12 show the air temperature of the three vegetational units maintaining closely approximate patterns as calculated and plotted on the basis of two-week periods.

Seasonal means of relative humidity in the shrub station are consistently above those in the less protected situations studied. The annual mean variation in relative humidity is also least here, a condition likewise exhibited in the estival and autumnal periods. The other two seasons, however, produce greater mean ranges of relative humidity in the shrub station than in the true prairie subsere station (humidity records for Station 2 secured for autumnal period only, Table 6). This is in apparent correlation with the air temperature values in these stations.

The most striking differences in measurable meteorological factors shown by the three vegetational units investigated in this study are those exhibited by the seasonal and yearly mean wind velocities (Table 16). Because of the

direct and biologically important correlation of wind with evaporation stress, these differences are worthy of particular note. Air movement values were at all seasons greatest in the true prairie subsere station, with the postclimax deciduous shrub station consistently showing the lowest values. While air movement values in the tall grass station at all times fell between those for the other two stations, they were markedly closer to those for the shrub (Figs. 11, 12), the steeper gradient maintaining between the true prairie subsere and the tall grass. The lowest seasonal mean wind velocity for Station 3 appeared in the estival period; the greatest discrepancy relative to Station 1 occurred in the prevernal-vernal. The annual mean wind velocity determined for Station 3 was 10.7% that for Station 1 and 45.6% that for Station 2; these values attest the greater efficiency of the shrubs in checking air movement at all seasons. The topographic differences of the stations, i.e., northwest slope of Station 3 and southwest exposure of Station 2, may have introduced complicating compensations which can not be evaluated.

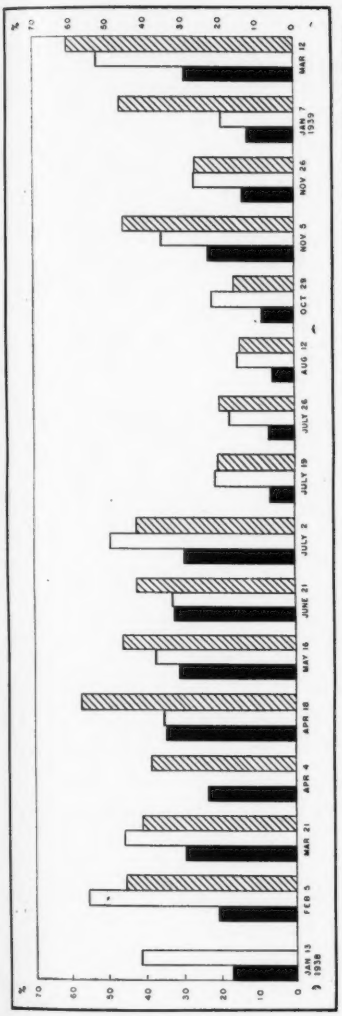
Sunset-sunrise readings on air movement were taken at various times during the estival and autumnal seasons of 1938. Total air movement values as low as 0.01 miles per night were recorded in the shrub station. During the same night 0.03 of a mile of wind was recorded in the tall-grass station, with 3.15 miles the total in the true prairie subsere station. Such a low, occurring between sunset of July 21 and sunrise of July 22, was an average of approximately 2 feet per hour. This may have been solely cold air drainage. Often on summer evenings, shortly after sunset, when the anemometer in the prairie subsere station would be motionless, the instrument in the shrub station would be turning slowly under the force of the cool air flowing down the ravine.

Probably no day passes when the prairie is without wind. Short periods of calm often occur during the day before approaching thunderstorms and their accompanying and often violent wind shifts.

Evaporation rates as measured by porous cup atmometers at 0.35 meters in the three situations show the expected gradient (Table 13). The estival mean for the tall-grass station is 58.8%, and that for the shrub station 46.5% of the mean for the true prairie subsere station. The rate at the 2 meter level in the shrub station (shrub stratum) approaches that of the prairie subsere station, being 86.2% of the latter. These meager data on evaporation rates show (Fig. 11) that a definite peak occurred during the two-week period ending August 15 in 1938, a time that showed one of the three recorded lows in relative humidity for that year, and, interestingly, corresponded with the period of highest mean temperature.

Heavy dews were common in the prairie during the summer of 1938. Only on nights when wind values were high was it possible to make sweep collections without the net becoming completely saturated with water.

Seasonal means of moisture content of the soil, expressed as per cent in excess of the hygroscopic coefficient, were consistently highest in the shrub station except in the autumnal period when that of the tall-grass station was slightly in excess of the shrub (Table 9; Fig. 13). Soil moisture values reached their lowest seasonal mean, 5.9%, in the true prairie subsere station during the autumnal season and the high of 47.3% in the shrub station during the prevernal-vernal period (Table 16).



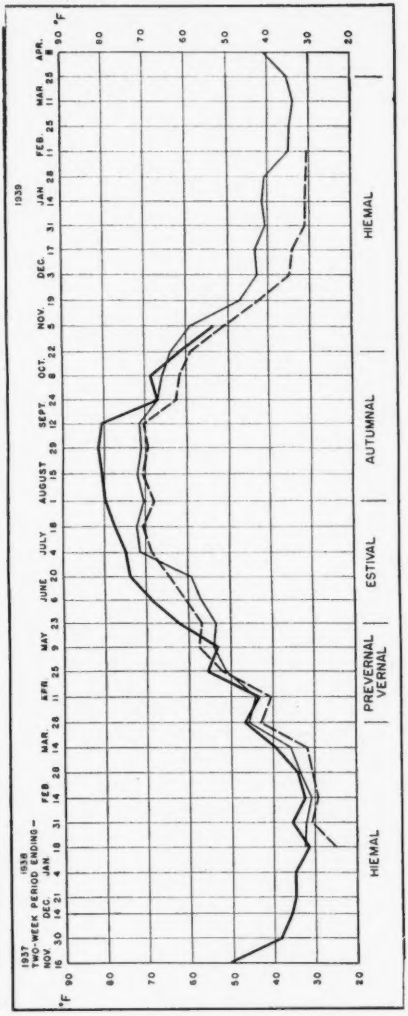


Fig. 13. (left).—Water content of soil, expressed as per cent in excess of the hygroscopic coefficient at a depth of 0 to 0.1 meter, on the dates indicated: Subseral true prairie (black bar); Postclimax tall grass (unshaded bar); Postclimax deciduous shrub (hatched bar).

Fig. 14 (right).—Temperature of the soil at 0.1 meter below the soil surface, expressed as mean °F. per two-week period, November 2, 1937 to April 8, 1939: Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line).

The estival mean soil temperature in Station 1 was 9.1°F. and 8.6° above that in Stations 2 and 3, respectively (Fig. 14). Station 3 produced the low mean soil temperature during the autumnal and hiemal periods but again exceeded Station 2 in the prevernal-vernal at which season it also exhibited its greatest mean range in soil temperature. These soil temperature phenomena are apparently in correlation with the amount of cover and the resultant decrease in insolation, the low annual mean of the shrub station further illustrating this feature. The fact that seasonal maximums in range of soil temperature are greater in the shrub station than in the tall-grass station for the hiemal and prevernal-vernal periods suggests that the vegetational cover of the tall-grass situation has a greater insulative effect upon the soil than that in the shrubs during these seasons. The situation is reversed, however, in the autumnal period, the differences in maximum range in soil temperature within these two stations then reaching 15.5°, while their maximum ranges are identical in the estival.

Inadequate but carefully secured information on light intensities in foot candles at the surface of the ground in the three stations (Table 14) shows that in full sunlight at midday the light intensity in the deciduous shrub station was approximately 20% of that in the subseral true prairie, while the intensity in the tall-grass area was slightly more than 30% of the intensity in the subseral true prairie (July 1, 1938).

On the basis of the environmental data gathered (albeit sometimes discontinuous or meager) and briefly reviewed here, general and comparative characterizations of the three habitats studied may be made in summary:

1. The true prairie subsere, the postclimax tall-grass, and the postclimax shrub stations showed, in the herb stratum, inconsistent and probably nonsignificant differences in mean air temperature values; the latter two stations showed, however, greater temperature ranges (maximum, mean maximum, and mean), with the widest ranges occurring in the tall-grass station, probably due to its southwest slope and consequent greater insolation.

2. Relative humidity was usually somewhat higher in the postclimax stations, although unexplained inversions of this gradient occurred.

3. The reduction of wind velocity at the herb level by the cover in both the shrub and the tall-grass station gave the most striking gradient of aerial factors.

4. Insolation was apparently greatest in the prairie subsere, least in the shrub station.

5. Evaporation stress, as measured in the herb stratum (late estival and early autumnal, 1938) was greatest in the true prairie subsere, least under the shrubs; evaporation rate values in the shrub stratum of the shrub station approached (once slightly exceeded) those recorded for the herb stratum of the prairie subsere. This environmental factor, being considered as a function (and index) of all other climatic factors to which terrestrial animals are subject (Blake 1926:48[412], Fichter 1939:197) furnished horizontal and vertical gradients which, in general, indicate the quantitative distribution of physical factors of the atmosphere through the three communities studied.

6. Correlative with the other environmental factors mentioned, available soil moisture was generally greatest in the shrub station, least in the prairie subsere.

Population Studies

Invertebrate animals in terrestrial habitats occupy places in time and space which are more or less inherent in the realization of their annual cycle of life processes. This ecological grouping, implemented by organic responses to conditions of the habitat in attempted fulfilment of the environmental needs of each species present, results in population structure. The differences in specific requirements, the changes in requirements of any given species as its life history unfolds, the responses to shifts in environmental optima, the motivations of innate behavior, the expressions of annuation and phenology—all these and probably many undiscovered forces—keep the structure of a community of active terrestrial invertebrates exceedingly fluid. Such a dynamic organization literally moves through time and space. This fluctuating chronological and spatial distribution is expressed in seasonal or aspect societies, horizontal differentiation and movement, and vertical groupings called stratal or layer societies which show both seasonal and diurnal changes, even in hibernation (Blake 1926:98[462]). These complex interrelationships of never-static forces and responses function to produce population phenomena which, albeit highly dynamic, are subject to both quantitative and qualitative analysis. The degree and fruitfulness of analysis depends, in part, upon cognizance of all environmental variables impinging upon the biota which is being subjected to examination. The known variables in any habitat are many; there are possibly as many unknown. Unfortunately, when the investigator enters a habitat to attempt his analysis of the animal community, he introduces another variable, a disturbing factor which he probably cannot measure; his presence and passing may alter the structure of the population in that given volume of space.

Despite the obvious overlaps of environmental factors and organic cycles, responses, and distributions, it is necessary to break down the time, the space, the forces, and the animal population into units suitable for measurement, analysis, and expression. This breakdown is an attempt to harmonize natural sequences and groupings with the expediencies of investigation and report. Any expression of the findings relative to one unit will, however, in some degree point out certain conditions in some or all of the other units of the breakdown, so integrated are the measurable phenomena. Thus, remarks on aspection will indicate some feature of annuation, certain stratal relationships, and horizontal groupings and re-groupings. Reports on stratification show seasonal and daily succession and *vice versa*. It is intended that the descriptive sections that follow, regardless of their headings, will present a generalized picture of the animal ecology of drought disturbed true prairie and its postclimax inclusions.

Considering, briefly, certain general characteristics of the invertebrate fauna of the three contacting vegetational complexes as studied from November 2, 1937, to April 8, 1939, it is evident that Homoptera constituted the numerically superior order of invertebrates studied, ranking first in the herb stratum of the true prairie subsere (Station 1), second in that stratum in the postclimax areas of tall grasses (Station 2) and deciduous shrub (Station 3), and third in the shrub stratum of the latter. The order Diptera ranked second numerically in the area investigated, being the most abundant order in the tall-grass and shrub stations, while ranking fourth in the true prairie. The third most abundant order taken in sweep samples was Coleoptera, ranking second in the

subseral true prairie, sixth in the tall grass and in the herb stratum of the shrub, and fourth in the shrub stratum of the latter station. Ants of the family Formicidae showed population values which ranked them in fourth place in the sweep collections, being third most abundant in the herb stratum of the shrub station, fifth in the true prairie, seventh in the tall grass, and fifth in the shrub stratum. In fifth place among all groups taken throughout all stations was the Orthoptera, including families Phasmidae, Acrididae, Tettigoniidae, and Gryllidae. Orthopterans ranked third in the herb population of true prairie and postclimax tall grass and eighth in both herb and shrub stratum of the shrub station. Bees and wasps, here considered as a group, were seventh in numerical importance in Station 1 herb collections, fifth in these collections in both Stations 2 and 3, but second in importance only to the Diptera in the shrub stratum. In the herb stratum of subseral true prairie, tall grass, and deciduous shrub, the order Hemiptera ranked eighth, fourth, and fourth, respectively, and occupied ninth place in the shrub stratum. Eighth in the series of major groups was Araneida, spiders ranking fifth in Station 1 herb, eighth in Station 2 herb, and seventh in both herb and shrub stratum of Station 3.

It is seen that Homoptera and Coleoptera were the numerically prominent groups in the herb stratum of subseral true prairie, stratal prevalents and subprevalents being in these two orders. Among the tall grasses, Orthoptera, Hemiptera, and Diptera were largely contributory to population trends, with ants assuming a brief, minor importance; prevalents here were a grasshopper and a plant bug, the subprevalent an ant. Under the shrubs Homoptera and Diptera combined to furnish the majority numbers; a leafhopper and an aphid assumed prevalent rank; two species of flies became subprevalent. It should be noted here that although large numbers of flies were taken in the postclimax shrub station, the number of species remained so high that prevalent values were never attained by any single species.

Comparing the findings for the herb stratum in the true prairie subsere with those for the same stratum in postclimax tall grass and postclimax deciduous shrub (Table 22; Figs. 15, 19, 23, 25), it is immediately apparent that (1) the total population curves for the two grassland stations are generally similar, but that the tall-grass population maintained a more uniform population level, especially as regards the major (early estival) peak, and (2) the total population curve for the shrub station is remarkably different than for either of the prairie stations; the extremely high autumnal peak in the herb stratum of the shrub community is one of the most striking features reported here. Relatively uniform throughout the estival and first half of the autumnal aspect, with a tendency to build up in the early autumn, it shows a marked decrease in late September, followed by the sudden and dramatic upsurge to the short-lived October high.

The two grassland habitats showed some similarities in ground surface population patterns (Figs. 22, 23). There were two peaks of total population (estival and autumnal) albeit not coincident; the autumnal peak was the greater in the tall-grass, the estival the greater in subseral true prairie. Ants and beetles furnished the numerical majorities in both stations, the prevalents and subprevalents being members of these two groups.

The ground surface population in the shrub station also showed two peaks,

but the second and autumnal high was nearly as striking as that for the herb stratum in the same station. Beetles and ants again figured to some extent in shaping the total population pattern.

ASPECTION

It has been shown (Carpenter 1937) that species of insects which hibernate as adults or late instars are active in the early spring "in the habitat where they spend the winter." Sweep collections made in the herb stratum of true prairie subsere, of postclimax tall grass, and of postclimax deciduous shrub on November 19, 1938, January 2 and 7, February 6, and March 12, 18 and 20, 1939, showed over-wintering insects active upon the dry winter vegetation on days when the maximum temperatures ranged from 43.0°F. to 68.0°F. McClure (1938:507) has reported that aerial collecting done "by means of a net attached to the front fender of an automobile" driven many times over a specified route near Danville, Illinois, during the period November 1, 1934 to May 1, 1935, took insects "when the temperature was 40°F. or above." General field observations on March 7 and 21, 1938, and on March 12, 1939, with maximum day temperatures of 53.0°, 82.5° and 61.0°, respectively, in the prairie, noted arthropods active in the air and on the vegetation, especially on south slopes and ravines with southward drainage. Flies, microhymenoptera, true bugs, grasshoppers, and beetles were in evidence, with many spiders

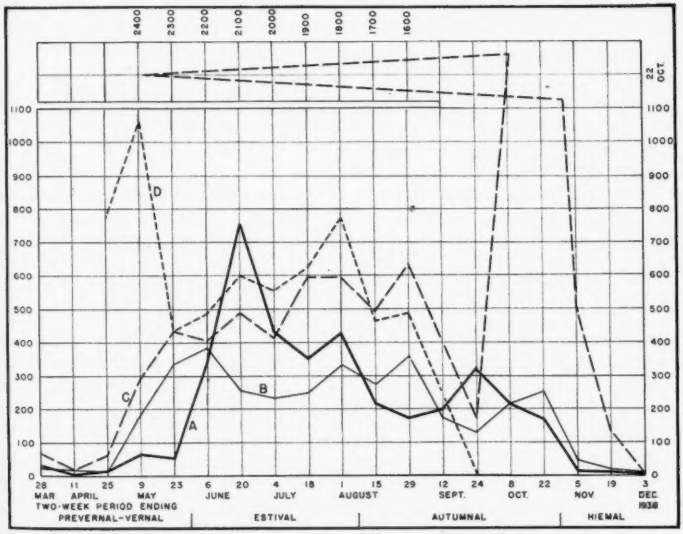


Fig. 15.—Trends of total populations of invertebrates (arthropods) in all aerial strata studied, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. *Herb stratum:* Subseral true prairie (line A); Postclimax tall grass (line B); Postclimax deciduous shrub (line C). *Shrub stratum:* Postclimax deciduous shrub (line D). (No collections in the shrub station during the two-week period ending September 12—see Tables 22 and 23.)

active on the surface of the ground. On the last date soil inhabiting larvae and earthworms were active at the surface of the soil. Dowdy (1944) found that soil invertebrates were influenced to move deeper into the soil in the fall at a temperature usually about 42°F. and that this same temperature caused their upward movement in the spring. Insects and spiders, finding hibernacula in the litter and the crowns of bunch grasses, such as the bluestems (Whelan 1927), and quickly responding to relatively brief daily peaks of air temperature as low as 43.0°, provide intervals of invertebrate activity above the surface of the soil at a time when plant life "except for fruits and seeds, is found almost entirely within the protecting soil and scarcely at all above it" (Weaver and Fitzpatrick 1934), and that in a dormant condition. Thus, with the advance of temperature values in the late hiemal period, characteristic prevernal activity begins before "the reappearance of young shoots from the awakening perennials" which has been characterized by Weaver and Fitzpatrick (1934) as the "only" organic process with which the new season is initiated. The prevernal aspect is first expressed faunistically.

Carpenter (1937), studying biotic communities in a large cattle range in central Oklahoma which was selected "as representative of the south-central mixed-grass prairies," found that "aspection . . . began earlier in the year in lower and sloping areas than in the high prairie, but proceeded more rapidly in the latter once activity had begun. Prevernal activity in the wooded ravines began as early as March 10 (1934) while the prairie itself showed little change in aspect until three weeks alter." Some agreement with this pattern of invertebrate activity is shown in the upland true prairie subsere and adjacent postclimax areas in eastern Nebraska. Sample collections made in the herb stratum during the two-week period ending March 28, 1938, showed population values of the shrub station to be in excess of those in the tall-grass and true prairie (Fig. 15), with values in the latter two being nearly identical. Illustrating the close correlation of temperature patterns and aspection as expressed by the invertebrate fauna, the shrub and prairie subsere curves of invertebrate populations show a distinct decrease in the two-week period following this initial rise, while the curve for the tall-grass station remains nearly constant. It will be noted (Fig. 11) that temperature curves show a decided low for this period, following which both temperature and invertebrate population curves tend consistently upward (Fig. 15). Greater protection from the high winds recorded during the two-week period ending April 11 (Fig. 11) in the tall-grass station, due to topographic position in relation to wind direction, may account for the maintenance of population levels in that station. Carpenter also noted the effect of protection from winds as a factor in initiating aspection in the prevernal period.

With the advent of the flowering period of *Prunus americanus* in late April and early May, the population values for the shrub stratum in the postclimax deciduous shrub station suddenly climb from nearly nil to the yearly high for that stratum (Fig. 15). As suddenly, near the middle of May, this population falls off, then renews its ascent with the initiation of the estival aspect and the period of anthesis of *Cornus stolonifera* to a not too distinct tertiary annual peak for the two-week period ending June 20.

Coincident with this poorly defined early estival peak in the shrub stratum are (1) the second of the four minor peaks of the herb stratum in the same

vegetational complex and (2) the yearly high for the true prairie subsere invertebrate population. This latter high is apparently correlated with the period of anthesis of most of the true prairie plants; Steiger (1934) states that the "high prairie has the greatest number of species flowering in June." At this time the population of the herb stratum of the prairie subsere exceeded that in the same stratum of the postclimax tall grass as well as the populations in both herb and shrub stratum of the postclimax shrub area. The population value for the tall grass had at this time markedly decreased, possibly indicating a movement of insect forms out of this situation where maximum flower production was to occur later (Steiger 1934) into the true prairie subsere where the maximum of anthesis had already been reached—a movement that may have in part accounted for the estival peak in the prairie subsere.

The most notable features regarding total populations of invertebrates above the ground surface in the three stations studied following the first week of July (1938) are (1) the secondary peak of abundance in the shrub stratum of Station 3 during the last two weeks of July, followed by a rather rapid decline to practically nil near the end of September, (2) the extremely high population values exhibited by the herb stratum in the deciduous shrub area during the middle of October (late autumnal period), and (3) the marked decline of populations in all aerial (epiphytic) strata subsequent thereto toward the low values characteristic of the hiemal. The almost total disappearance of invertebrates from the shrub stratum coincides with and apparently results from the unusually early loss of leaves by *Prunus, Cornus* and other shrubs already mentioned. Population curves for all aerial strata considered show coincident and definite declines of various magnitudes for the two-week period ending August 15, 1938, the period marked by (1) the estival-autumnal temperature peak, (2) a recognizable low in fortnightly mean values of relative humidity, (3) a distinct peak of evaporation rate, and (4) a minor high in wind velocity values (Fig. 11). Epiphytic strata in the shrub and tall-grass stations showed gains in the invertebrate populations in the following two-week period whereas the population in the herb stratum of the true prairie subsere continued its decline. Haying operations beginning on August 13 probably accounted for the latter decrease, since sweep collections were made in both mowed and unmowed areas. During the next three to four weeks the herb stratum populations in the tall-grass and shrub communities again declined while that of the true prairie subsere tended upward, possibly in response to renewed growth of grasses following mowing. Subsequent to this time (September 4, 1938) the true prairie subsere curve tends downward to the hiemal low, the tall grass shows a late autumnal peak, and the curve that represents population values in the herb stratum of the shrub station soars to the remarkable autumnal high of 2,382 specimens per unit collection, a value 315% that of the estival high of the herb stratum in true prairie subsere (second highest peak) as determined in this study. This autumnal high thence gives way rapidly to the low hiemal values.

The quantitative relationships of litter (Table 24) and soil (Table 25) populations to aerial populations are illustrated in Figure 16 on a seasonal basis. It is principally notable that litter values are high during seasons when aerial populations are low, i.e., hiemal and prevernal-vernal, and low when aerial activity is in the ascendancy. Pearse (1946) has stated that in decidu-

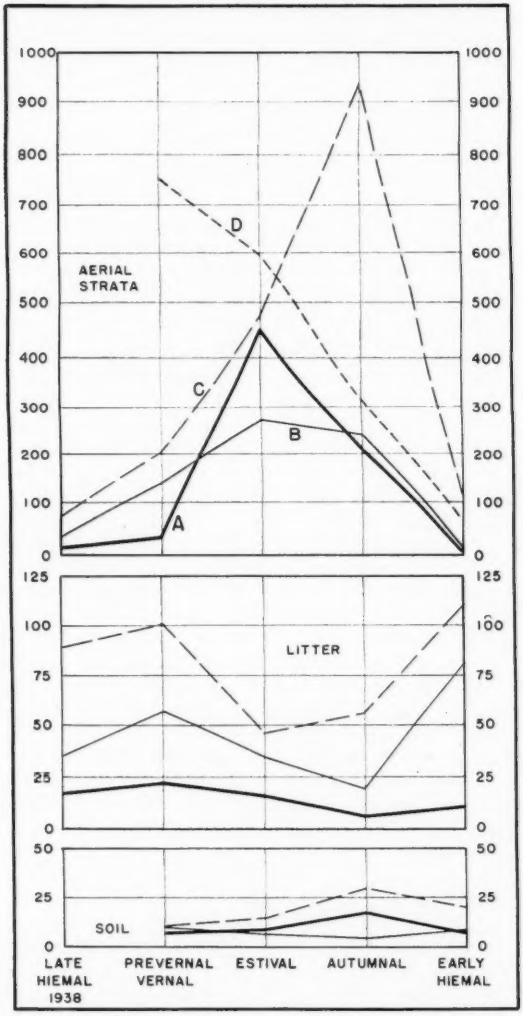


Fig. 16.—Seasonal trends of invertebrate populations expressed as average numbers per unit collection per seasonal period, late hiemal to early hiemal inclusive, 1938. *Aerial strata:* Herb stratum of subseral true prarie (line A); Herb stratum of postclimax tall grass (line B); Herb stratum of postclimax deciduous shrub (line C); Shrub stratum of postclimax deciduous shrub (line D). *Litter and soil strata:* Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line).

ous forest "soil moisture appeared to be more effective in controlling numbers of animals present than variation in temperature," a condition also described by Blake (1931:526).

Studies by means of alcohol pitfalls on the invertebrates inhabiting the surface of the ground, carried on between April 8 and November 4, 1939, show seasonal population curves (Table 26; Fig. 18) closely comparable to those of epiphytic strata just reviewed. Here, however, the population peak in Station 1 occurred during the first half of July (Fig. 17) rather than during mid-June as in the herb stratum in the preceding year, the Station 2 autumnal peak was two weeks earlier than in the herb stratum of that station in 1938, and the Station 3 autumnal peak occurred during early September rather than late October, the latter period being marked by the outstanding shrub station high previously noted. These discrepancies were possibly, if not probably, due to unmeasured differences in the habitats under the influence of aberrant climatic conditions, principally drought.

The most striking single feature regarding all total populations so far considered is the high autumnal peak in the postclimax deciduous shrub community.

Seasonal averages of invertebrates per unit collection in the herb stratum (Table 23; Fig. 16) show (1) a distinct estival high in the subseral true prairie station, (2) a much less marked estival high in the tall-grass station with an autumnal peak of slightly less value, (3) the strikingly high autumnal peak in the deciduous shrub area, and (4) in the shrub stratum of this station the suddenly attained prevernal-vernal peak of abundance.

Collection averages of Homoptera in the herb stratum of true prairie subsere, i.e., Station 1 and substations, show the advent of this order in considerable numbers during the two-week period ending May 9 (1938), the middle of the prevernal-vernal period (Table 22). Two peaks of abundance are attained, a mid-estival peak during the two-week period ending June 20, and a lesser mid-autumnal peak during the twelve-day period ending September 12 (Fig. 19). The Homoptera do not show a definite peak of abundance in the postclimax tall grass (Station 2 and substation) although prevernal-vernal activity appears closely comparable to that in Station 1. In the postclimax deciduous shrub complex (Station 3 and substations) two well defined peaks of abundance occurred in the herb stratum, the first during the two-week period ending August 29, the second between October 8 and 22 (Fig. 25). In this station Homoptera appeared in the sweeps about two weeks earlier

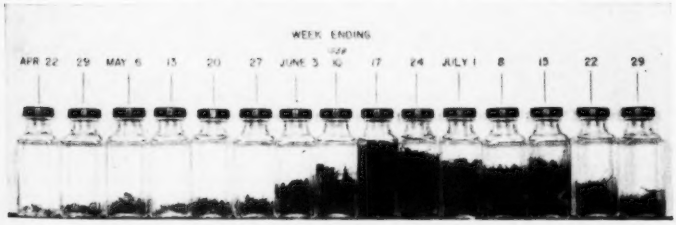


Fig. 17.—Bottles of invertebrates taken by the alcohol pitfall in the true prairie subsere station showing the early estival increase in numbers and volume, with a subsequent decrease, the peak in volume preceding the peak in numbers by two weeks.

than in the other communiites studied, showing, in fact, recognizable epiphytic population values during relatively warm winter days. In the shrub stratum of the shrub station (Table 23) prevernal activity of Homoptera began during the two weeks ending April 25, a population high being attained near the close of the estival period, July 18 to August 1 (Fig. 27). Homoptera were taken in very small numbers in the litter samples of all stations, were not in

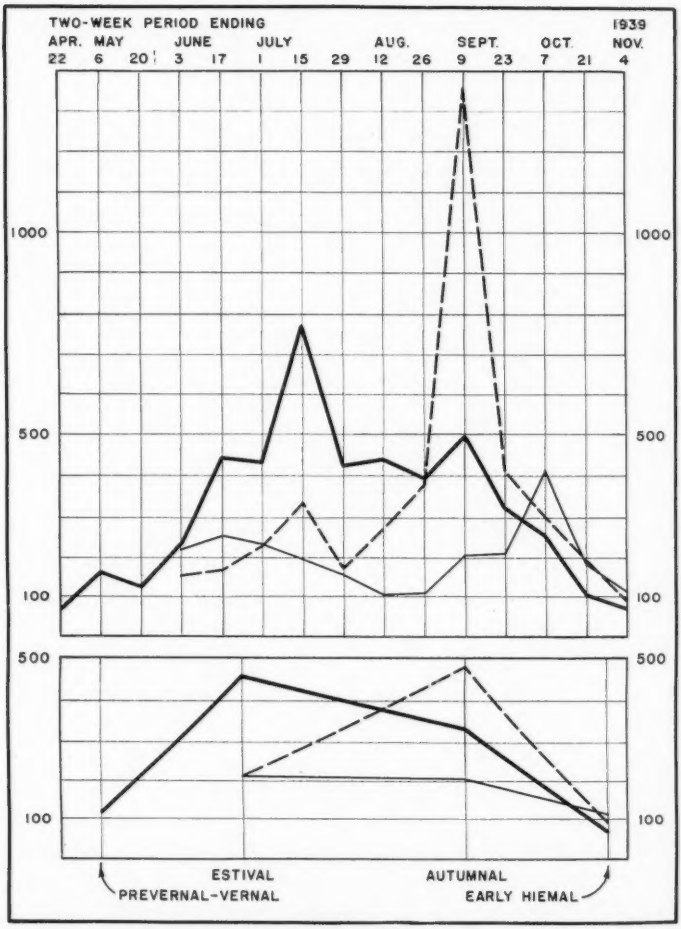


Fig. 18.—Population trends of invertebrates in the soil surface stratum, as indicated by alcohol pitfall collections, expressed as total numbers taken per two-week period (upper section) and as seasonal averages per unit collection (lower section). *Total population:* Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line).

any case retrieved by the soil washer, and were not considered as soil surface forms in the pitfall studies.

Diptera showed year-round activity (Table 22). Sweep collections made in the herb stratum on winter days when the temperature was at 43.0°F. or

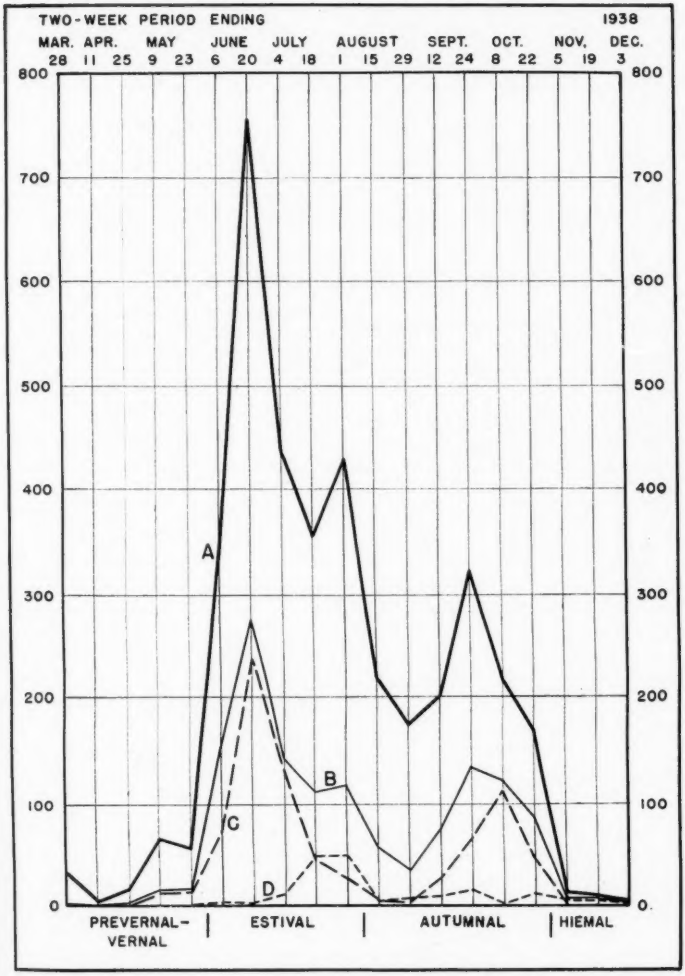


Fig. 19.—Population trends of invertebrates (arthropods) in the herb stratum of subseral true prairie, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. Total population (line A); Homoptera: leafhoppers, etc. (line B); *Balclutha abdominalis*, a leafhopper (line C); *Delphacodes* sp., a leafhopper (line D).

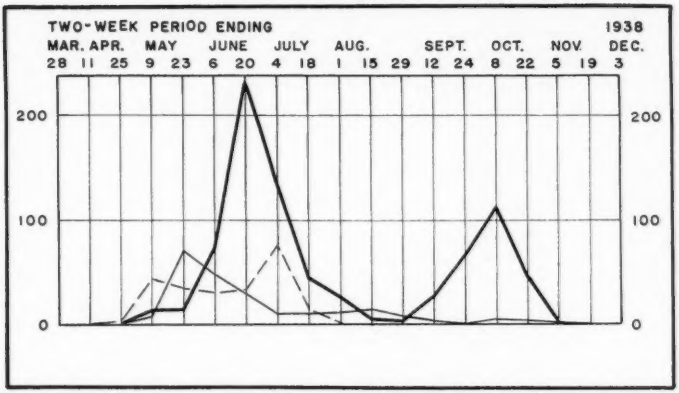


Fig. 20.—Population trends of *Balclutha abdominalis*, a cicadellid leafhopper, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. *Herb stratum:* Subseral true prairie (heavy solid line); Postclimax tall grass (light solid line); Postclimax deciduous shrub (broken line).

above, usually secured flies. Their numbers consequently built up rather suddenly in the prevernal-vernal aspect, producing an early estival peak in the herb community of true prairie subsere during the fortnight ending June 20, with a second and lesser mid-autumnal peak in this situation during the first half of September. Three poorly defined peaks are shown by flies in the herb stratum of the postclimax tall grass. In the postclimax shrub area Diptera presented important quantitative values, showing a more or less distinct high during the two weeks ending July 18 with a marked low late in September, thence producing a population peak which surpassed that of all other orders in all other communities studied, a population value largely responsible for the important autumnal peak of total populations already pointed out (Fig. 25). Flies were abundant among the flowers of *Prunus*, producing a prevernal-vernal high for the order in the shrub stratum during the two weeks ending May 9 (Fig. 27). Two lesser estival peaks appeared in mid-June and late in July. No flies were taken in the shrub stratum in September or in March. Diptera were rarely found in litter collections, none at all in soil samples, and are not here included in the pitfall studies.

Beetles (Table 22) played little or no part in the prevernal-vernal herb society in true prairie subsere, but with the advent of the estival season near the end of May climbed rapidly to a marked population high during the two-week period ending June 20 (Fig. 21). A second and very minor late autumnal peak appeared between October 8 and 22. Prevernal-vernal activity of Coleoptera in the herb stratum began considerably earlier in the ravine stations (2 and 3). Early estival highs appeared in these stations coinciding with that in Station 1, although being much less distinct. An autumnal high occurred in the latter half of August. In the shrub station an early estival peak was also produced, followed by a low and a second high of nearly equal magnitude during the two weeks ending July 18. In the shrub stratum of

this station (Table 23) the year's peak of beetle population came at the time of anthesis of the wild plum during the fortnight ending April 25, maintaining nearly equal values until the end of the blossoming period at the advent of the estival aspect (Fig. 27). Conforming to the general population picture,

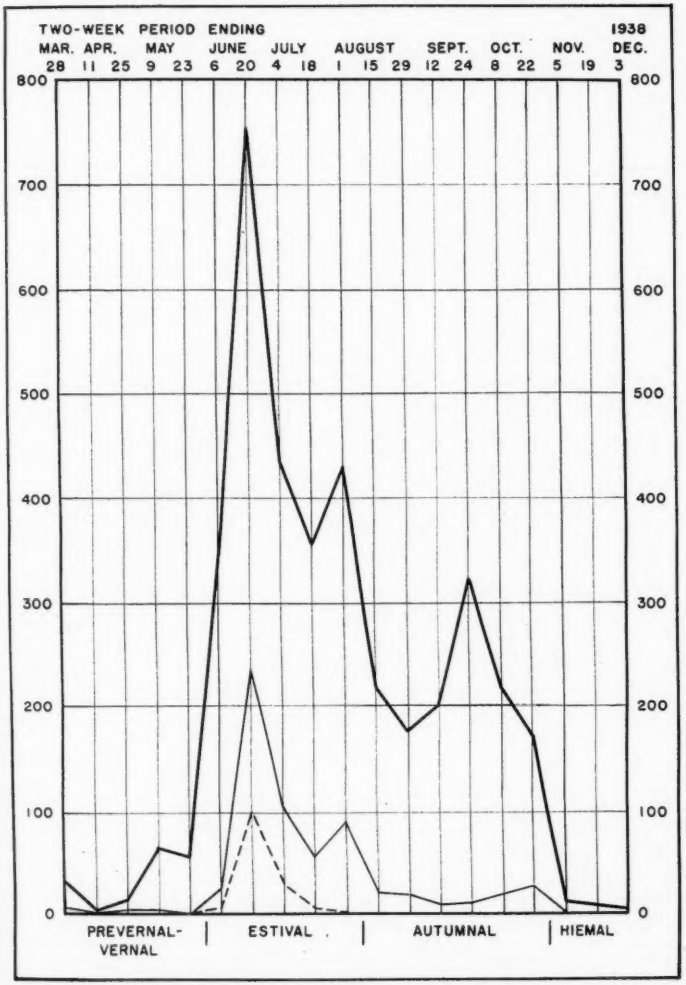


Fig. 21.—Population trends of invertebrates (arthropods) in the herb stratum of subseral true prairie, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. Total population (heavy solid line); Coleoptera: beetles (light solid line); *Pachybrachys litigiosus,* a chrysomellid beetle (broken line).

however, the beetles produced a second though lesser peak during the two weeks ending June 20. No beetles were taken in the shrub stratum in September. Beetles occurred in important numbers in the pitfall collections in all three stations. More numerous in these collections of ground surface forms in the shrub site than in the other stations, the group here reached its maximum of abundance in early autumn, July 29 to August 12, 1939 (Fig. 28). In the true prairie subsere where they were next most abundant the beetles showed a marked population peak in the ground surface stratum during the fortnight ending June 17 (Fig. 22) at which early estival period they also reached their greatest peak of abundance in the tall-grass station (Fig. 24).

Ants (Table 22) appeared in the herb sweeps in the true prairie subsere

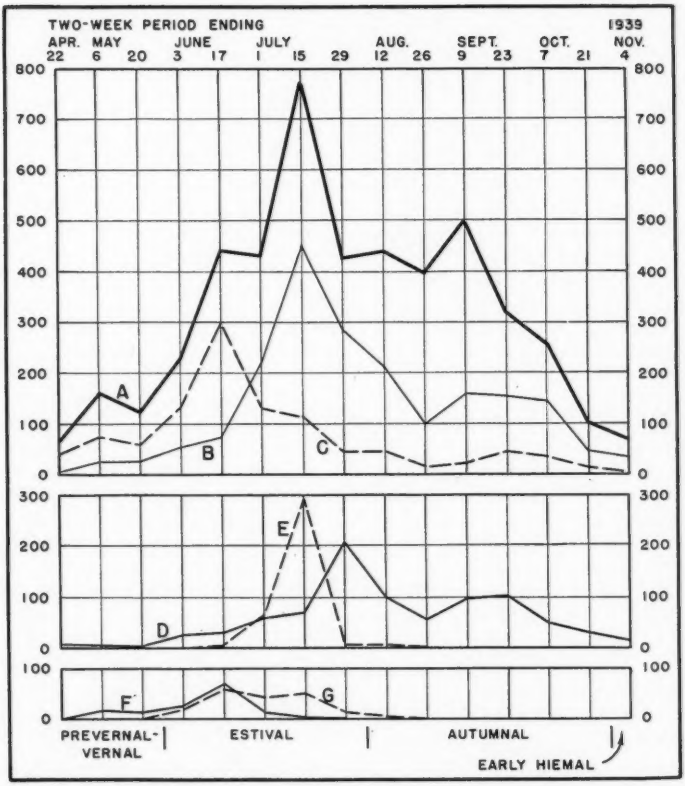


Fig. 22.—Population trends of soil surface invertebrates in subseral true prairie as indicated by alcohol pitfall collections expressed in total numbers taken per two-week period from April 8 to November 4, 1939. Total population (line A); Hymenoptera: ants and velvet ants (line B); Coleoptera: beetles (line C); *Crematogaster lineolata*, an ant (line D); *Dorymyrmex pyramicus*, an ant (line E); *Amara* sp., a carabid beetle (line F); *Eleodes opaca*, a tenebrionid beetle (line G).

and postclimax tall grass late in April and about two weeks earlier in that stratum in the shrub area. Significant peaks appeared in Station 2 in late August (Fig. 23) and in Station 3 in late October. In the shrub stratum (Table 23) ants produced a prevernal-vernal peak in late April and early May and a second peak during the fortnight ending June 6. The reasons for these peaks are not clear. Ants showed relatively important values in litter collections with prevernal-vernal highs occurring in Stations 1 and 2, and a late hiemal-pervernal-vernal high in Station 3. It must be remembered, however, that "the population of the ground is in patches and not uniform" (Shackleford and Brown 1929), and that all data based on litter samples is, therefore, subject to distortion. Unimportant numbers of ants occurred in soil samples. In the pitfall studies more ants were taken than were specimens of any other major group of invertebrates, the greatest number in the shrub station collections. In the true prairie subsere a definite peak of abundance occurred during a two-week period ending July 15 (Fig. 22), sharp peaks not appearing in the other two stations until the two weeks ending October 7 (Figs. 24 and 28).

Certain of the grasshoppers, wintering over in late instars, were usually in evidence on warm winter days. These species, however, appeared to be much less abundant than those which passed the hiemal period in the egg stage, thence emerging as small nymphs with the coming of spring. Significant numbers of young grasshoppers (family Acrididae) appeared simultaneously in all stations during the fortnight ending May 9 (Table 22). Newly hatched walking sticks (family Phasmidae) appeared in the upland true prairie subsere on May 16. The orthopteran population, composed chiefly of these two families until mid-August, with the tettigoniids assuming important numbers from mid-June till the advent of winter, produced early estival and late estival peaks in the herb stratum of the prairie subsere, a fairly well defined late vernal peak and a secondary autumnal peak in the tall-grass station (Fig. 23), and a single, weakly expressed, late vernal high in the shrub station. Orthopterans were most abundant in the shrub stratum during the two weeks ending July 18 (Table 23). Significant numbers of orthopterans were not taken in litter or soil samples, and takes in the pitfalls were relatively low though consistent. Because of the saltatory abilities of grasshoppers the takes in sweep net collections are undoubtedly subject to discrepancies which alter the true picture of the order's population values.

The winged forms of the order Hymenoptera are often active on warm winter days in protected situations. In this study they appeared in large numbers in the shrub station in late April and early May, in the tall-grass station about two weeks later, and in the upland true prairie subsere station during the two weeks ending June 6, at which time their yearly peaks for that society were reached (Table 22). Bees and wasps produced no observable peak in the Station 2 herb stratum, but exhibited a relatively enormous late autumnal population in that stratum in the shrub station during the two weeks ending October 22. Two marked peaks of abundance of winged Hymenoptera appear in the shrub stratum (Table 23), the first from April 25 to May 9, the second and somewhat higher from July 4 to 18 (Fig. 27), these highs corresponding to the periods of blossoming of *Prunus* and *Cornus* respectively, giving quantitative expression to the already well known affinities of these insects for flowers.

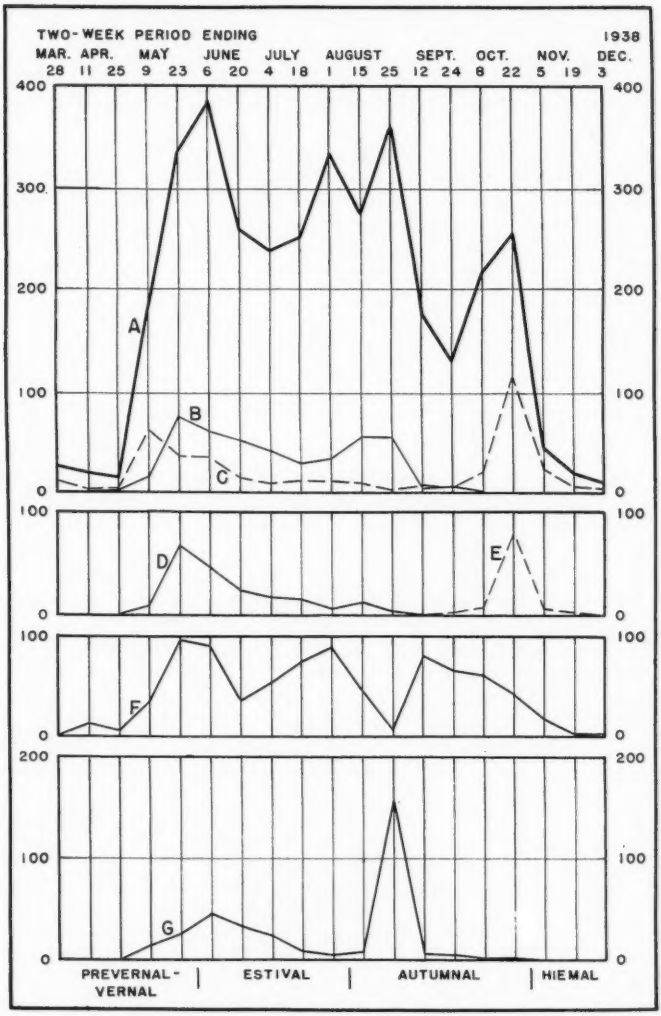


Fig. 23.—Population trends of invertebrates in the herb stratum of postclimax tall grass (ravine site), expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. Total population (line A); Orthoptera: grasshoppers (line B); Hemiptera: bugs (line C); *Melanoplus bivittatus*, a grasshopper (line D); *Lygus pratensis*, a bug (line E); Diptera: flies (line F); Formicidae: ants (line G). The early autumnal peak in ant numbers was forced by a single winged species, *Pheidole bicarinata* (see Table 28).

The order Hemiptera has often been pointed out as importantly abundant in the true prairie. Clements and Shelford (1939) state that "an abundance of Hemiptera characterizes the prairie." In this study these bugs (Tables 22, 23) were usually in evidence, although not in numbers which would conform to such a characterization. Sharply defined high peaks of abundance appeared in the herb sweeps in the tall-grass (Fig. 23) and shrub stations during the

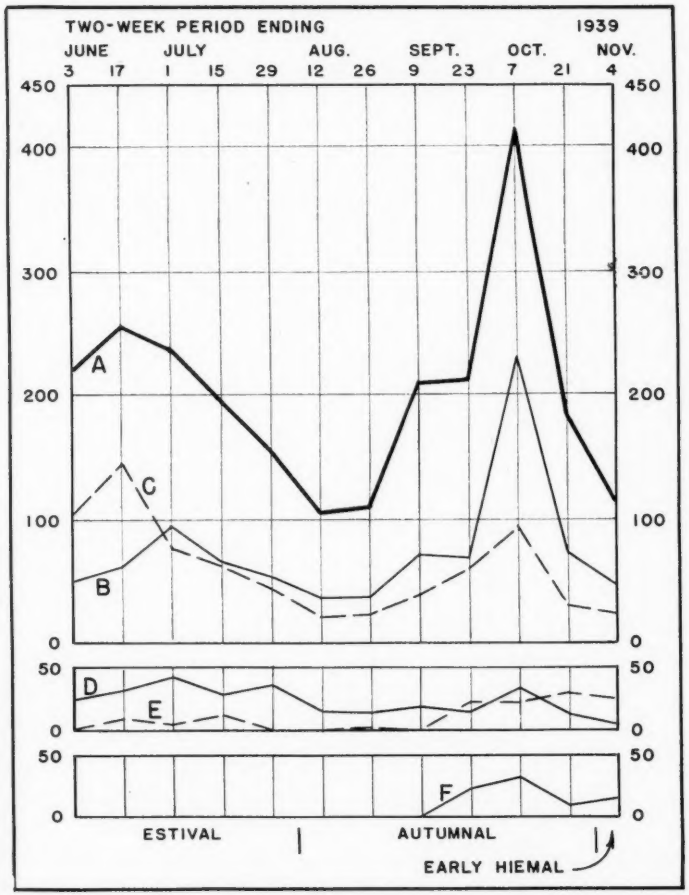


Fig. 24.—Population trends of invertebrates of the soil surface stratum in postclimax tall grass (ravine site) as indicated by alcohol pitfall collections and expressed in total numbers taken per two-week period, May 20 to November 4, 1939. Total population (line A); Hymenoptera: ants and velvet ants (line B); Coleoptera: beetles (line C); *Crematogaster lineolata*, an ant (line D); *Prenolepis imparis*, an ant (line E); *Agonoderus pallipes*, a carabid beetle (line F).

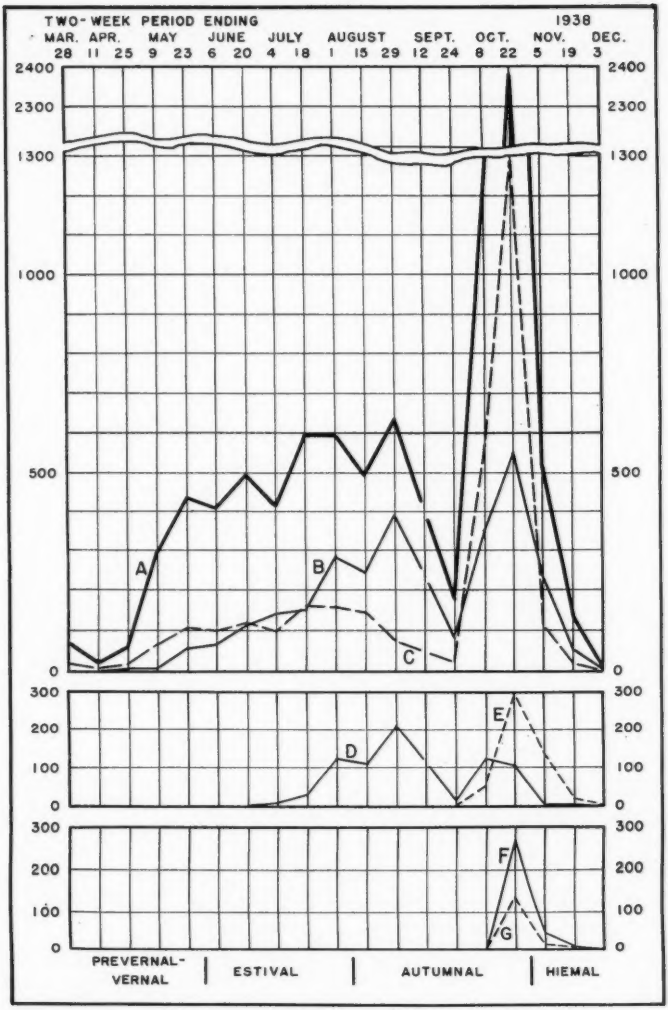


Fig. 25.—Population trends of invertebrates in the herb stratum of postclimax deciduous shrub (ravine site), expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. Total population (line A); Homoptera: leaf hoppers, etc. (line B); Diptera: flies (line C); *Dikraneura abnormis*, a leafhopper (line D); *Anoecia graminis*, an aphid (line E); *Oscinella coxendix*, a chloropid fly (line F); *Elachiptera costata*, a chloropid fly (line G). (No collections during the two-week period ending September 12—see Table 22.)

two-week period ending October 22, followed by a marked increase of bugs in the litter samples in the fortnight following. Here is presented probably the most convincing example offered by this study of the horizontal movement of grassland insects into forest margin conditions and their subsequent descent

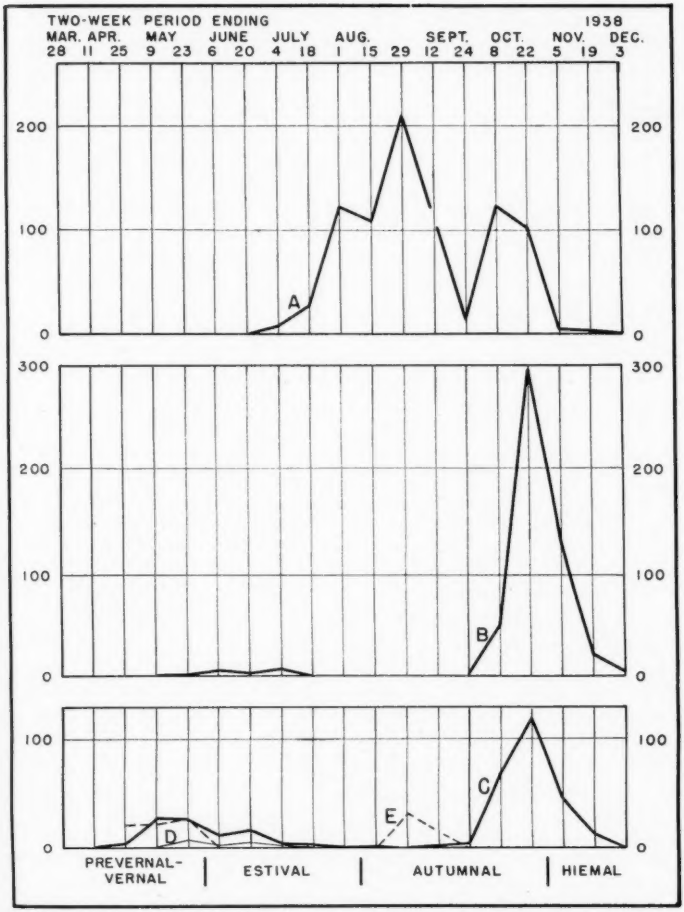


Fig. 26.—Population trends of three prevalent species, expressed as average numbers per unit collection (day sweeps) per two-week period, March 14 to December 3, 1938. *Dikraneura abnormis*, a leafhopper, in the herb stratum of the postclimax shrub station (line A); *Anoecia graminis*, an aphid, in the herb stratum of the postclimax shrub station (line B); *Prenolepis imparis*, an ant: In the herb stratum of the postclimax shrub station (line C), in the herb stratum of the postclimax tall-grass station (line D), in the shrub stratum of the postclimax shrub station (line E). (No collections in the shrub station during the two-week period ending September 12—see Tables 22 and 23.)

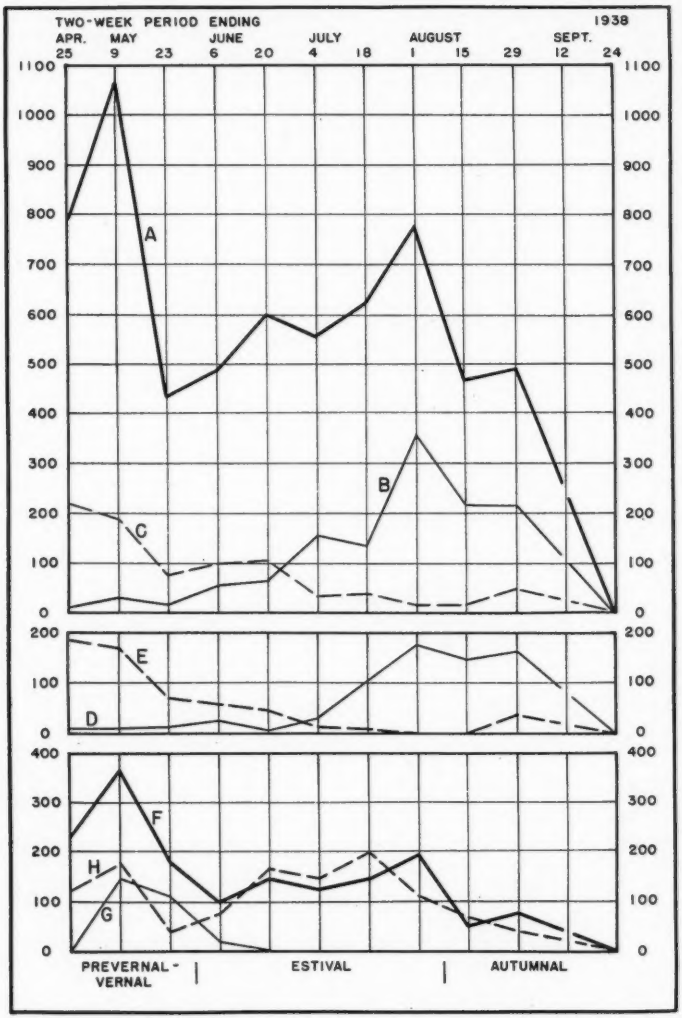


Fig. 27.—Population trends of invertebrates (arthropods) in the shrub stratum of postclimax deciduous shrub, expressed as average numbers per unit collection (day sweeps) per two-week period, April 11 to September 24, 1938. Total population (line A), Homoptera: leafhoppers, etc. (line B), Coleoptera: beetles (line C), *Erythroneura* sp., a leafhopper (line D), *Chalcoides fulvicornis*, a chrysomelid beetle (line E), Diptera: flies (line F), *Tachydromia maculipennis*, an empidid fly (line G), Hymenoptera (winged): bees and wasps (line H). (No collections during the two-week period ending September 12—see Table 23.)

into hibernating cover at the close of the autumnal aspect, as pointed out by Weese (1924) and others. Very low numbers of hemipterans were taken in the alcohol pitfall in the true prairie subsere during the entire period of that study, and in the tall-grass site until late October, when somewhat larger numbers appeared. In the shrub station pitfall, however, a very high hemipteran population was recorded during the two weeks ending September 9, 1939. This high is comparable to the late autumnal peak just described for the herb stratum of the preceding year, resulting from the high values produced by a single species of cydnid bug, to be discussed later. Such marked high points on the curve of total population have been pointed out by Blake (1926) to be apparently "due to the presence of certain particular species whose numbers attain a maximum, rather than to any general increase of any considerable number of species making up the population." Fichter (1939) noted population characteristics of this type in Wyoming spruce-fir forest, a condition that lends significance to the determination and scrutiny of prevalent species.

Spiders (Tables 22, 23) of several species appeared in all but one of the hiemal sweep collections in the herb stratum of the deciduous shrub station, and in this community their prevernal activity was much in advance of that in the tall grass and the true prairie subsere, producing a peak of abundance during the fortnight ending May 23. A second peak in this community coincided with the only peak of spider abundance occurring in the tall-grass station, that of August 15 to 29. The population of Araneida in the tall grass thence decreased rapidly while the population in the herb stratum of the shrub station dwindled rather slowly. In the true prairie subsere maximum abundance occurred during mid-September. The curve then tended sharply downward. Recognizable population peaks were not produced by spiders in the shrub stratum. Spiders were notably numerous in the litter collections in the hiemal period only. Values in the pitfall collections exhibited a marked uniformity throughout, a single, possibly significant peak occurring in the prairie subsere in the two-week period ending August 26.

Larval forms of Coleoptera, Lepidoptera, and Neuroptera, which must be arbitrarily considered here as a single group (Tables 22, 23), produced their highest combined population values in the herb stratum of Station 1 during the fortnight ending July 4 and in Station 2 during the preceding two weeks, while in Station 3 two well defined and much higher peaks were attained during the two-week periods ending May 23 and July 4. In the shrub stratum the maximum of population was reached between May 9 and 23. Litter values of this group are particularly high in the shrub station with the greater numbers occurring in the hiemal period. In the tall-grass litter samples, highs are shown in the prevernal-vernal and hiemal periods, while only the prevernal-vernal collections from the true prairie subsere yielded significant numbers of larvae. Pitfall values were, however, highest for larvae in this latter station, with a distinct peak occurring for the two-week period ending September 9.

Lepidoptera (Tables 31, 41), while commonly observed as apparently abundant in restricted areas of the prairie tract, such as over the alternes of western wheat-grass during its period of anthesis, appeared in all collections in insignificant numbers.

Seasonal aspects in grassland "are determined primarily by the seasonal

march of habitat factors, of which temperature and length of day are the most important. So far as the palnts themselves are concerned, they may be in evidence throughout the entire growing season, but they give character to the matrix of vegetation only during the period of flowering" (Weaver and Clements 1939).

"The culmination of fruition and maturity of the autumnal blooming forms and late maturing grasses occur in September and October. After this time there is a gradual deterioration of the vegetation, which is hastened by repeated frosts. . . . The leaves of the grasses dry in place on the erect stems" . . . and plant life "is found almost entirely within the protecting soil. . . . In late winter and spring many mosses and numerous lichens are to be found on the damp soil between the tufts of sod" (Weaver and Fitzpatrick 1934).

The prevernal-vernal aspect.—Late March introduced the prevernal-vernal aspect in the true prairie subsere and the adjacent and contacting areas of tall grass and deciduous shrub. Insect and arachnid species which had spent the winter in the adult or late instar stages furnished a sudden surge of visible life during the warm days of this awakening period. Spiders, carabid beetles, and nymphal grasshoppers in late stages of development were especially evident on the surface of the ground. Although sweep net collections in the dry herbage of upland true prairie subsere during this period in 1938 revealed superior numbers of Diptera, the number of species of flies was so great that among the lesser, but at this time rapidly ascending numbers of Homoptera, occurred the prevernal-vernal prevalent in this stratum. The leafhopper *Balclutha abdominalis* (V.D.) (Tables 27, 29), did not, however, attain this rank until late in the aspect, and was at no time as conspicuous to casual observation as other and less abundant forms. In the litter the carabid beetle, *Amara* sp. (Tables 27, 30) was prevalent. Soil and pitfall collections* showed this beetle to be the prevalent species in the shallow layers of the soil and upon the ground surface. In the ravines within the postclimax tall-grass complex the dipterans were even more abundant than in the high prairie. Hemipterans, especially *Piesma cinerea* Say (Tables 27, 30) and *Lygus pratensis* (Linn.) (Tables 27, 30), stirring from their hibernacula, showed much activity among the old grass stems, the former giving subprevalent numbers. The cicadellid, *Balclutha abdominalis,* exhibited subprevalent values and other homopterans were here in marked abundance, but nymphs of *Melanoplus bivittatus* (Say) (Tables 27, 30), the two-lined locust, assumed prevalent rank. The chinch bug, *Blissus leucopterus* (Say) (Tables 27, 30), showing some low values in the sweep collections, was subprevalent in the litter stratum where the enchytraeid worms of the genus *Fridericia* (Tables 27, 30) prevailed at this season, while *Amara* sp. showed prevalent numbers in the soil.

Invertebrate species were even more abundant in the postclimax deciduous shrub areas of the ravines, with prevernal activity beginning in this complex well in advance of that in both true prairie subsere and tall grass. Flies were likewise here the most abundant order at this season, the chloropid, *Madiza* sp. (Table 28), showing subprevalent numbers. With ants and homopterans showing approximately equal population values in the herb stratum, *Balclutha abdominalis* assumed the prevalent role in this community as well as in the

* All pitfall records taken in 1939.

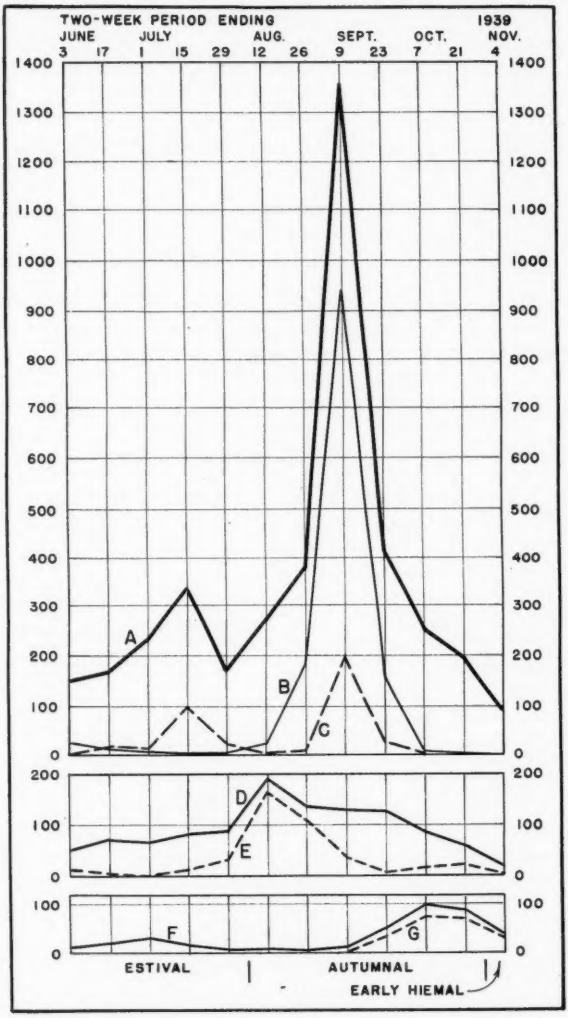


Fig. 28.—Population trends of invertebrates of the ground surface stratum in postclimax deciduous shrub, as indicated by alcohol pitfall collections and expressed in total numbers taken per two-week period, May 20 to November 4, 1939. Total population (line A); *Geotomus robustus*, a cydnid bug (line B); *Leiobunum* sp., a phalangid (line C); Coleoptera: beetles (line D); *Ataenius cognatus*, a scarabeid beetle (line E); Hymenoptera: ants and velvet ants (line F); *Prenolepis imparis*, an ant (line G).

subseral true prairie herb stratum. The typically woodland fly, *Tachydromia maculipennis* Walker (Table 28), attained subprevalent rank. The prevernal-vernal season constituted the high total population period for the shrub stratum. Here among the flowers of *Prunus americanus*, adults of Diptera, Coleoptera, and Hymenoptera were especially abundant, as were larvae of numerous species of insects. The chrysomelid beetle, *Chalcoides fulvicornis* (Fabr.) (Tables 27, 31), although less conspicuous, was here the prevalent species. In the deep litter beneath the shrubs *Fridericia* was active in prevailing abundance. In the soil small numbers of the pupoid snail, *Gastrocopta armifera* (Say), were found; more thorough studies of this stratum might have showed this small gastropod to be prevalent.

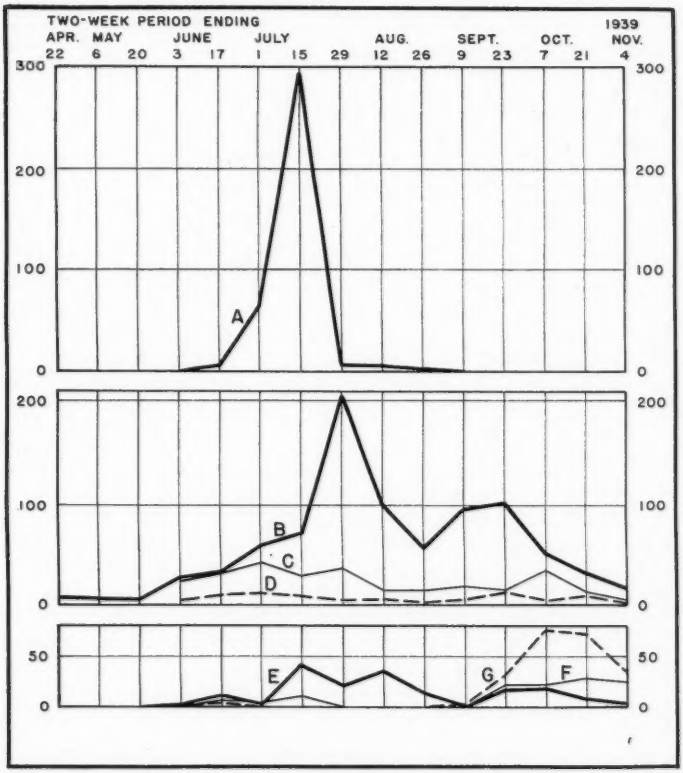


Fig. 29.—Population trends of three prevalent species of ants (Formicidae) in the ground surface stratum, as indicated by alcohol pitfall collections and expressed in total numbers taken per two-week period, May 20 to November 4, 1939. *Dorymyrmex pyramicus:* Subseral true prairie (line A). *Crematogaster lineolata:* Subseral true prairie (line B), postclimax tall grass (line C), postclimax deciduous shrub (line D). *Prenolepis imparis:* Subseral true prairie (line E), postclimax tall grass (line F), postclimax deciduous shrub (line G).

The estival aspect.—During the last week of May, with the spikes of June grass beginning to open, needle grass in full bloom and the wild alfalfa characterizing the subdominant vegetation, the estival period witnessed a rapid increase in the total population of invertebrates in the herb stratum and on the surface of the ground in the true prairie subsere. Homoptera and Coleoptera characterized this fauna in the herb layer, with Diptera and Orthoptera present in marked abundance. Prevailing was the leafhopper, *Balclutha abdominalis*, with the psyllid, *Aphalarea veaziei* Patch, the fulgorid, *Delphacodes* sp., the chrysomelid beetle, *Pachybrachys litigiosus* Suffr. and *Orthocis* sp., a cioid beetle, showing subprevalent numbers (Tables 27, 28, 29). Conspicuous in the first half of this aspect was *Pachybrachys luridus* Fabr., the walking stick, *Diapheromera veliei* Walsh, and the May beetle, *Phyllophaga lanceolata* (Say), the latter abundant on the wild alfalfa. *Delphacodes* became markedly abundant after mid-July (Tables 27, 29), at a time when *Pachybrachys litigiosus*, *P. luridus* and *Phyllophaga lanceolata* were showing marked decreases. Invertebrate numbers were low in the litter and soil strata in the estival period, with *Fridericia* prevailing, while the ant, *Dorymyrmex pyramicus* Roger (Tables 27, 29), characterized the ground surface population in company with the subprevalent tenebrionid beetle, *Eleodes opaca* (Say) (Table 28).

Balclutha abdominalis attained the rank of estival prevalent in the herb stratum of the postclimax tall-grass areas, although the Diptera presented the greatest abundance of all invertebrate orders, especially those flies of the family *Muscidae*. The cicadellid, *Macrosteles divisus* (Uhl.) (Table 28), showed subprevalent values along with *Delphacodes* sp. and *Pachybrachys litigiosus*. In the soil the carabid, *Amara* sp., still prevailed, sharing subprevalent rank with the ant, *Crematogaster lineolata* Say (Tables 27 and 29) in the litter where the annelid, *Fridericia*, had attained prevalent rank. On the surface of the ground *Crematogaster lineolata* produced distinctly prevailing numbers during the estival period in 1939.

Within the shrub station *Balclutha abdominalis* still held prevalence in the herb layer, with the cicadellids, *Empoasca* sp. and *Dikraneura* sp., and the empid fly, *Rhamphomyia* sp., in subprevalent rank (Table 28). Adding distinction to this society, and indeed to the forest margin character of the postclimax deciduous shrub, was the typically woodland fly genus, *Dolichopus*, and the woodtick, *Dermocenter variabilis* Say. Producing prevalent numbers in the shrub stratum was *Erythroneura* sp., a cicadellid which was confined to this society (Tables 27, 31).

Fridericia still prevailed in the litter, with the ant, *Ponera coarctata pennsylvanica* Buckley, subprevalent (Table 28). *Gastrocopta armifera* continued to be present in small numbers in the shallow layers of the soil. Vividly characterizing the estival invertebrate fauna of the soil surface in the deciduous shrub station was the phalangid, *Leiobunum* sp. (Tables 27, 31). This harvestman came into prominence in mid-July and again in early September, being superseded in the latter instance, however, by the hemipteran, *Geotomus robustus* (Uhler) (Tables 27, 31), thereby attaining a prevalent rank only in the estival. Accompanying *Leiobunum* sp. was the dung beetle, *Ataenius cognatus* Lec. (Tables 27, 31), as a subprevalent.

The autumnal aspect.—Early August and the advent of the autumnal period in the grassland and its associated postclimax areas, was marked by the gradual

end of anthesis of the estival plants, the beginning of flowering of the coarse composites, and the loss of much of the green color in the grasses. With this distinct change came a decrease in populations of the invertebrate fauna of the true prairie subsere. Characteristic of the August decline was the walking-stick, *Diapheromera veliei.* Still prevalent in the herb stratum of true prairie was *Balclutha abdominalis,* with the minute brown scavenger beetle, *Corticaria* sp., the chloropid fly, *Oscinella minor* Adams, the gryllid, *Oecanthus niveus* (DeG.), and the ants, *Tapinoma sessile* Say, *Aphaenogaster fulva aguia* Buckley, and *Pheidole bicarinata* Mays, ranking as subprevalents (Table 28). The ground beetle, *Amara* sp., in this season assumed prevalent rank in both soil and litter and the ant, *Crematogaster lineolata,* was now prevailing upon the surface of the soil.

The tarnished plant bug, *Lygus pratensis,* attained autumnal prevalence in the tall-grass sites where the subdominant *Aster multiflorus* was conspicuously in flower and characterizing the herb stratum. *Delphacodes* sp. acquired subprevalence in this community at this season, sharing this rank with an undetermined species of cecidomyiid fly.

The downward movement of the Hemiptera into the litter began in the autumnal aspect. The tingid bug, *Piesma cinerea,* became prevalent in the litter during this season while the tarnished plant bug showed subprevalent values. *Amara* sp. and *Crematogaster lineolata* still prevailed beneath the surface and on the surface of the soil, respectively, while a second carabid, *Agonoderus pallipes* Fabr. (Table 28), acquired subprevalence at the soil surface.

Homoptera and Diptera thoroughly dominated the picture of the markedly high autumnal invertebrate population in the herb stratum of the postclimax deciduous shrub area. With *Dikraneura abnormis* (Walsh) (Tables 27, 31) in the prevalent role, the fly, *Oscinella coxendix* (Fitch), the cicadellid, *Empoasca* sp., the fulgorid, *Delphacodes* sp. (Table 28), the aphid, *Anoecia graminis* Gillette and Palmer (Tables 27, 31), and an undetermined fly, produced subprevalent populations. The high October peak of total population produced by the arthropods in this community, already recounted, is largely the result of increases in these six species populations. *Ataenius cognatus* continued its subprevalence upon the surface of the soil, a rank which it shared with the ant, *Prenolepis imparis* Say (Tables 27, 31), while *Geotomus robustus* was also prevailing in the soil stratum.

The hiemal aspect.—The acquisition of prevalence by an invertebrate in aerial strata during the hiemal aspect is, of course, intermittent and dependent upon temperature conditions. The high frequency values of the fulgorid, *Delphacodes* sp., in herb sweep collections in the true prairie during the winter and its superior though low numbers accord it hiemal prevalence in this community. *Piesma cinerea* prevailed in the litter in the true prairie, while *Amara* sp. retained its prevalence in the soil. *Crematogaster lineolata* maintained its autumnal prevalent rank at the soil surface into the early hiemal period (1939).

Hemiptera characterized both the herb and litter stratum in the tall grass during the hiemal aspect. Among the grasses during early November *Lygus pratensis* showed prevalent values, with the pentatomid, *Thyanta custator* Fabr., a conspicuous subprevalent. *Nabis ferus* Linn. was in evidence. Chinch bugs, *Blissus leucopterus,* moved into the litter in such numbers as to accord

this species prevalent rank in that stratum where *Piesma cinerea* and the coccinellid beetle, *Hippodamia convergens* Guer., were present at subprevalent values (Table 28). The soil surface invertebrate fauna of early winter was characterized by *Prenolepis imparis,* and *Amara* sp. continued as soil prevalent.

Retaining a considerable portion of the subprevalent values which it built up in the late autumn, *Anoecia graminis,* an aphid, assumed the prevalent role in the herb stratum of the deciduous shrub area during the early hiemal. *Empoasca* sp. and *Delphacodes* sp. retained their subprevalent values acquired in the late autumn, and *Lygus pratensis* here became a subprevalent. Prevailing in the litter of the shrub station in this aspect was the enchytraeid worm, *Fridericia* sp., with the hemipterans, *Piesma cinerea, Blissus leucopterus, Orius insidiosus* Say, the staphylinid beetle, *Oxypoda* sp., and the ant, *Leptothorax curvispinosus ambiguus* Emery, exhibiting subprevalent values. At this season the soil harbored prevalent numbers of *Ataenius cognatus* and subprevalent numbers of *Geotomus robustus,* while *Prenolepis imparis* prevailed upon the surface of the ground during the post-autumnal transition.

STRATIFICATION AND DIURNATION

Stratal relationships of invertebrate animals have been investigated and reported upon for pine-hemlock forest in Maine and deciduous forest (winter) in Illinois by Blake (1926), for the "tree layer" of maple-red oak forest in Illinois by Davidson (1930), for spruce-fir forest in Wyoming by Fichter (1939), for "young elm-maple stage" of deciduous forest in Tennessee by Dowdy (1941), and for oak-hickory forest in Missouri by Dowdy (1947). The concensus of these authors is, in general, that stratal distribution of invertebrates occurs rather regularly in forest in response to vertical gradients of physical factors which probably operate together with certain biological factors, with seasonal and diurnal changes in strata and stratal composition being evident.

In the herbaceous cover of open grassland, obviously much shallower than forest cover, any aerial strata resulting from factor gradients are probably by comparison also much shallower. Stratification of physical factors in prairie veegtation can be discerned and measured, but is studied faunistically with greater difficulty than in forest, or even shrubby cover. Don B. Whelan conducted certain ecological studies within the prairie tract reported on here, and he has kindly furnished me with unpublished data which is helpful in this consideration of stratification. Whelan took 699 readings with a hand anemometer from March 10, 1928 to September 14, 1929, inclusive. His three sets of readings were made in feet-per-minute at five feet above the ground surface, at 14 inches above the ground surface, and at the ground surface in high and low prairie. Considering his readings at the five foot level (which was above the tops of the herbs) as base value (i.e., 100%), the wind movement values at the 14 inch level in high prairie through the late hiemal, prevernal-vernal, estival and autumnal aspects were 75%, 70%, 58%, and 53% respectively; at the ground surface 46%, 37%, 11%, and 5% respectively; at the 14 inch level in the low prairie, 71%, 76%, 60%, and 53% respectively, and at the ground surface 29%, 31%, 13%, and 4% respectively. Yearly mean averages of Whelan's data show air movement values at the 14 inch and ground surface levels to be 63% and 23%, respectively, of that at five feet above the ground in the high prairie, and 65% and

20% in the low prairie. It is apparent that the gradient became steeper as the growing season progressed, the greatest differences occurring in the autumnal aspect. Readings were taken several times when the anemometer registered 0 feet per minute at the ground level (which is actually about 0-6 inches above the ground surface) while the other two levels showed considerable movement. For example, on August 8, 1929, in the high prairie (corresponding to Station 1 of this study) the reading at the ground surface, 14 inch, and five foot levels were, respectively, 0, 310, and 856 feet per minute.

Whelan gathered further data which indicate recognizable stratification of physical factors in prairie. He exposed porous cup atmometers at ground level and at 12 inches above the ground surface. The values which he secured throughout the estival and autumnal season (May 24 to October 11) show evaporation rates at the ground level to have averaged 72% of those at the 12 inch level. It is not known whether these data on evaporation were gathered in 1928 or 1929, or whether the values furnished me were standardized; the general indication is to be considered reliable, however.

In the present study the entire depth of the herbaceous cover in the three stations was treated as a single stratum. Inasmuch as this is primarily a study of grassland invertebrates, and since the herb stratum received the most attention, a more or less detailed analysis of the physical factors and invertebrate populations of that stratum in the true prairie subsere is appropriate. Phenomena of aspection and horizontal distribution will be further illustrated as well. The conditions and processes of stratification and diurnation will, of course, be more strikingly shown in studies made in the deciduous shrub habitat.

Fortnightly means of air temperature (as determined for the purposes of this study) rose to above 40°F. in the herb stratum of true prairie subsere during the two-week period ending March 28 and fell below this level during the comparable period ending December 3 in 1938 (Fig. 11). The two weeks ending August 15 produced the annual temperature peak, with a fortnightly mean of 83.7° and an absolute maximum of 112.0°. Two rather well defined depressions appear in the temperature curve, the first for the two-week period ending April 11, the second for the 12-day period ending September 24. Accompanying the April depression in temperature was the year's greatest fortnightly peak of mean wind velocity, and one of three fairly well defined lows in relative humidity. Accompanying the September depression was one of three well expressed lows in wind velocity. During this approximately 250 day period with fortnightly means of temperature above 40°F., absolute temperatures ranged from 21.5° to 112° (a range of 90.5°), fortnightly maximum ranges varying from 34.5° to 62.0°.

Fortnightly means of relative humidity for this period appear quite constant, varying from 54.1% to 79.6%, with a maximum range, however, of over 80% (16.5% to nearly 100%), with this range occurring in the two-week period ending March 28. The lowest range of humidity values, 44.5%, was recorded during the fortnight ending June 20.

Sweep collections in the herb stratum of this drought disturbed true prairie during the hiemal period yielded arachnids and insects when temperatures were above 40°F. for even short periods. Spiders, short-horned grasshoppers, hemipterans such as plant bugs, damsel bugs, and stink bugs, homopterans, especially *Delphacodes* sp., coleopterans (principally flea beetles), dipterans

(principally an undetermined ephydrid in March), and very few winged Hymenoptera were taken. Unit collections (50 sweeps) in the hiemal season took from 0 to 47 specimens, the latter number appearing in the collection for March 21, 1938; 55.3% of this population was composed of the undetermined ephydrid fly. The average population value per unit collection for the fortnight ending March 28 (end of hiemal aspect) was 31 (Table 22); that for the following two-week period (beginning of prevernal aspect) was 2.5. This low coincided with the depressed temperature and relative humidity values and the annual peak in wind velocity. From this marked low at the onset of the prevernal aspect in the true prairie subsere, the population of invertebrates in the herb stratum built up to the annual (estival) peak for the two weeks ending June 20 (Fig. 15) with a collection average of 756. Homoptera and Coleoptera, constituting 67.7% of the total numbers (36.4% and 31.3%, respectively) were likewise at their annual population peaks (Figs. 19, 21). These two orders continued to contribute the greatest numbers to the population, in part forcing two subsequent lesser peaks, one for the fortnight ending August 1, the other for the 12-day interval ending September 24. This third and autumnal peak is perhaps the more noteworthy of the lesser two, with Homoptera contributing 42.4% of the average collection value 323. Diptera had reached its peak in the preceding two-week period and was at this autumnal high forming 16.4% of the total population. Spiders were at their peak in this stratum and station, comprising 11.8% of the total numbers collected. Orthoptera were of some importance in the late July peak. Within six weeks following the autumnal high all group populations had fallen off to typical hiemal low value levels. There is some possibility that these two lesser peaks may have resulted from a rather deep "notch" in what would have been a single autumnal high, as a result of immediate and lagging effect of the August 1-15 high temperatures and wind velocities and low relative humidity (Figs. 11, 15).

Into this picture of strato-seasonal activity prevalent species, as determined in this study, fit with comparable patterns. Figures 19 and 21 show the population curves of two homopteran prevalents and coleopteran subprevalents which forced the peaks of population for their respective orders, and also forced or contributed largely (so far as species are concerned) to the total population peaks. Figure 20 compares the population curves of *Balclutha abdominalis* (Homoptera, Cicadellidae) in the only stratum in which it was taken—the herb stratum of the three stations studied; its superiority in this stratum of the true prairie subsere is marked; its preference for this stratum is obvious.

Much more conspicuous in this situation than *Balclutha abdominalis* were the walking stick, *Diapheromera veliei*, the chrysomelid beetles, *Pachybrachys litigiosus* (Table 28), and *P. luridus*, and the scarabeid, *Phyllophaga lanceolata*. Yet only *Pachybrachys litigiosus* attained even subprevalence. The top day collections of both *Balclutha abdominalis* and *Pachybrachys litigiosus* were made in the afternoon of June 17; 103 of the beetles were taken in this sample, a number only 23.6% of the homopteran prevalent's value.

This partial description of the invertebrate population of the herb stratum in true prairie subsere through the various seasonal aspects has so far been based upon daytime samplings. Collections designed to sample the populations during (1) comparatively low temperature and high relative humidity

values in the presence of light, (2) high temperature and low relative humidity values in the presence of light, (3) comparatively high temperature and low relative humidity values in the absence of light, and (4) low temperature values and high relative humidity values in the absence of light, were made at irregular intervals from June 12 to October 29, inclusive, in 1938. Tables 32 and 33 and Figures 30 to 35, inclusive, indicate the time limits in which these collections were made, which for convenience in the text will be called day A.M., day P.M., night P.M., and night A.M., respectively. Table 17 to 21, inclusive, present the physical factor data relative to these collection periods, and Figures 30 to 35, inclusive, graphically show certain of these values. The first week of the hiemal period as previously delimited is included with the autumnal in these studies on diurnation.

Through the period June 12 to October 29, 1938, total population values as determined by sweep net collections in the herb stratum of true prairie subsere averaged highest in the night P.M. collections when temperature and relative humidity values averaged more or less intermediate in their ranges and wind values averaged a marked low; mean population values were lowest in the night A.M. collections, when temperature values were lowest, relative humidity values at a marked high and wind values intermediate (Fig. 30). It must be noted, however, that (1) the temperature averages for day A.M., night P.M., and night A.M. show relatively little range (about 4.6°F.), while the day P.M. temperatures averaged from about 15° to 20° above the others, (2) relative humidity means for the day A.M. and the night P.M. periods approach each other while those for day P.M. (low) and night A.M. (high) are nearly 38% apart, and (3) that the night P.M. values of wind velocity show a well defined low. Obvious shifts in physical factors occurred in the herb stratum; coincident with them were fluctuations in the total numbers of invertebrates taken by a standardized sampling method. On the basis of averages, the early part of the night, when (of the four periods considered) temperature and humidity conditions were intermediate but wind values quite low, produced a population high in the herbs; late in the night when temperature values were slgihtly lower than during the preceding period, but when wind values were again building up and relative humidity reached its daily (*diel* of Carpenter 1938:80) peak, the population dropped in a rather steep gradient to the daily low.

Determining and graphing these values (as available) separately for the estival and autumnal seasons, mean temperature and relative humidity are seen to retain much the same patterns, except that day P.M. relative humidity values were notably lower in the autumnal period. On the contrary, population patterns did not remain the same for the two seasons; the population decrease from a night P.M. high to a night A.M. low is even more striking (the loss amounting to 45.4%) than in the two-season averages. In the autumn the night P.M. total population retains its ascendancy, but is only slightly greater than that for the night A.M.; the two day population averages are likewise nearly identical but notably less than those for the night. In other words, the daily high and low are both produced in the night during the estival period, and a plateau high is produced in the night in the autumn (Fig. 30).

The average values used in this consideration, as based on relatively long periods (seasons), are compared with the same environmental and population

values as ascertained and graphed (1) for the four-week period ending July 4, 1938 (mean collection values), and (2) for four unit collections within a 51-hour period, 8:00 A.M. June 17 to 11:00 A.M. June 19 (actual collection values). These temperature, humidity, and total population curves retain

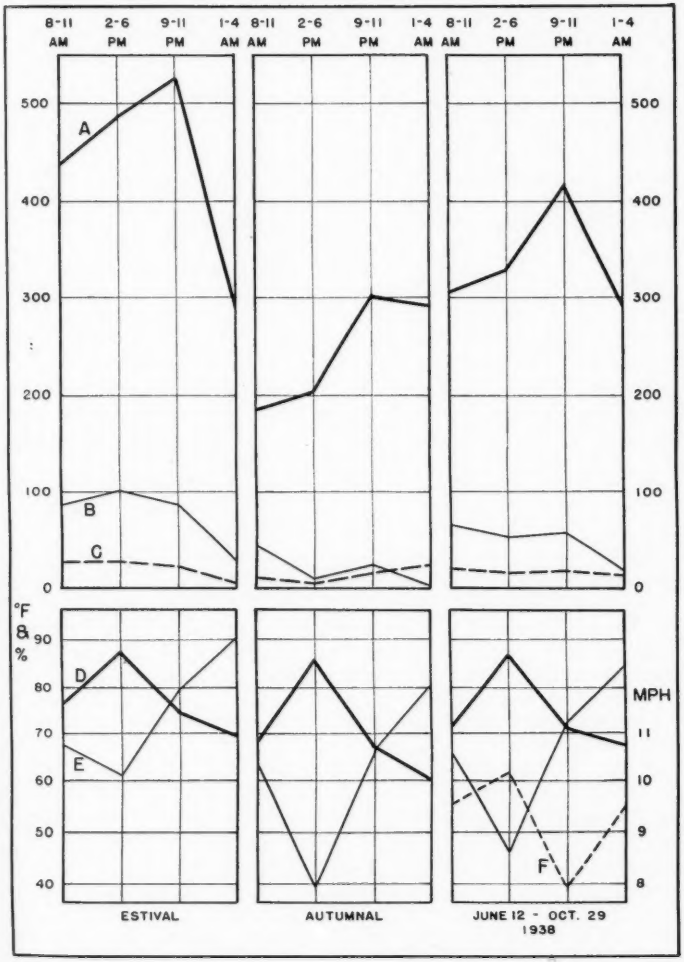


Fig. 30.—Diurnal and nocturnal values of invertebrate populations, temperature, and relative humidity in the herb stratum of subseral true prairie, and of wind at Lincoln, Nebraska, expressed as means for the periods indicated. Total population (line A); *Balclutha abdominalis,* a leafhopper (line B); *Delphacodes* sp., a leafhopper (line C); Temperature (line D); Relative humidity (line E); Wind velocity (line F).

essentially the same pattern as those for the season that encompassed these short periods (Fig. 31).

Such apparent fluctuations in quantitative structure of invertebrate groupings within a daily cycle suggest the probability of changes in qualitative structure, expressed through (1) variations in relative numbers of the many kinds of community components, and (2) sojourns by certain species into this stratum only during certain periods of the 24-hour cycle. Indications of such community phenomena are offered by prevalent and subprevalent species. For example, during the estival aspect the fulgorid, *Delphacodes* sp. (presumably a single species), retained a population ranging from 24.1% to 30.2% that of the cicadellid, *Balclutha abdominalis*, in the day A.M. and P.M. and night P.M. collection periods (Fig. 30); in the night A.M. period, although both *Delphacodes* and *Balclutha* declined, the former lost in relation to the latter, showing population values 18.5% those of *Balclutha*. Still more striking ratios were found in the values representing the entire period of study, including both seasons, *Delphacodes* maintaining values from 28.0% to 35.8% those of *Balclutha* through the day and first half of the night, but, despite slight decreases, showing values 70.6% those of *Balclutha* in the night A.M. samples. In the autumnal period inversions of these two species populations occurred within the daily cycle, and *Delphocodes* held ascendency over *Balclutha* in the night A.M. collections by a ratio of about 10:1. These population values are admittedly small; they might not be considered statistically valid; they do, however, show population trends and are indicative of changes in community structure during the daily cycle. Further indications are offered by comparison of the population values of *Balclutha abdominalis* and the subprevalent chrysomelid beetle, *Pachybrachys litigiosus* (Fig. 31), in which case higher population values were available for consideration. Comparable ratios of these two species are seen in the average-per-collection values for a four-week period and the actual collection values in a 51-hour period; most striking are the latter. The numbers of the subprevalent beetle taken in the day A.M., day P.M., and night P.M. samples were 43.7%, 23.6%, and 22.1%, respectively, those of the prevalent leafhopper. But in the night A.M. collection an inverse ratio appears and the leafhopper's abundance in the herb stratum was 44.3% that of the beetle.

Some comparisons of findings in this stratum with those of other strata in the same station are in order.

Data on the litter and soil populations in the true prairie subsere station are too meager to warrant any reliable comparative analysis. It may be briefly stated that litter populations exhibit lows during the estival and autumnal aspects and highs in the hiemal, with some buildup over the hiemal level during the early hiemal and prevernal periods, though this was not strikingly so in the true prairie subsere (Fig. 16). Soil populations appeared to attain a peak in the autumnal aspect; the values secured are probably too low to be reliable. Those conditions are probably the function of movements into and out of hibernacula, inadequately measured in this investigation.

Although the data were gathered in the following year, elucidating population values were determined for the ground surface stratum in the prairie subsere station. That the herb and ground surface strata were not studied simultaneously is unfortunate (resulting from belated employment of the alcohol pitfall method) and introduces a weakness in the examination of

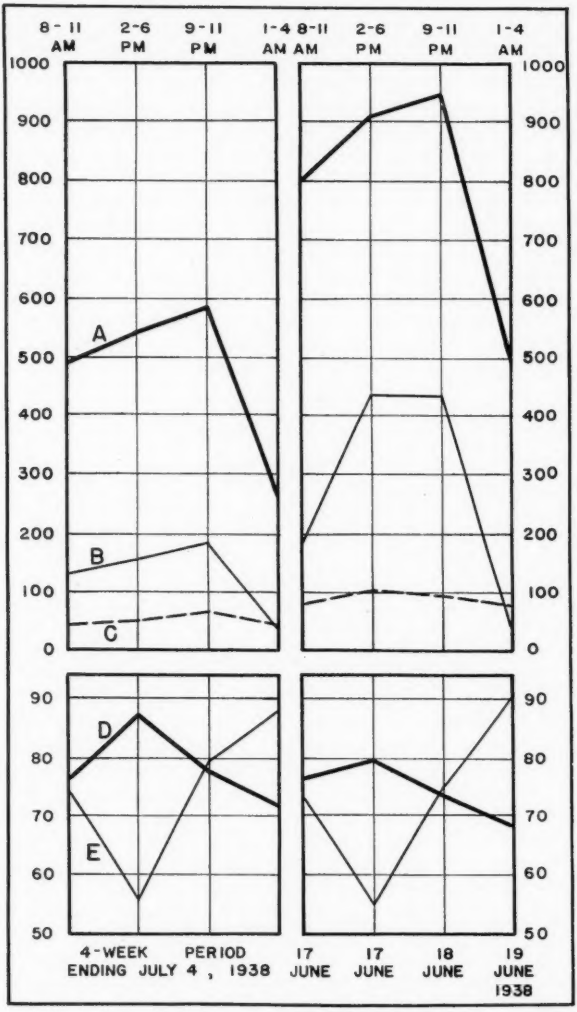


Fig. 31.—Diurnal and nocturnal values of invertebrate populations, temperature, and relative humidity in the herb stratum of subseral true prairie, expressed as means for the intervals indicated within the four-week period ending July 4, 1938, and (for the animals) as actual numbers taken in four unit collections within a 51-hour period, June 17 to 19, inclusive, 1938. Total population (line A); *Balclutha abdominalis*, a leafhopper (line B); *Pachybrachys litigiosus*, a chrysomelid beetle (line C); Temperature (line D); Relative humidity (line E).

stratal behavior attempted here. Any expressions of annuation that might have existed are hidden, but none the less complicating.

In 1939 the ground surface population of the true prairie subsere as measured in this study attained a distinct peak in the two-week period ending July 15 (Fig. 18). This high shows a lag of approximately four weeks behind the 1938 population high of the herb stratum of the same station. This comparison cannot, of course, be conclusive, being based on the records for two different albeit consecutive years. That both strata show an estival peak of population does seem significant, however; the time difference may be actual in any year, or may in this instance have been the function of the rapidly changing nature of the prairie vegetation and aberrant weather picture already outlined. It is of interest to note that the ground surface population here shows a second lesser and autumnal peak somewhat in keeping with a lesser peak in the herbs in the preceding year.

Ants and beetles were largely responsible, as groups, for the estival peak, less so for the autumnal peak (Fig. 22). Coleoptera forced the total population up during the vernal and early estival period to a "peak within a peak" for the two weeks ending June 17 (Fig. 22). Then, as ants were coming into prominence, beetle population values fell off. At their June 17 peak of abundance beetles comprised 67.6% of the take, ants 17.2%. A month later ants were obviously forcing the total population peak (estival), comprising now 58.1% of the total collection value, beetles making up 15.0%.

The species which forced these trends were the prevalent ants, *Dorymyrmex pyramicus* and *Crematogaster lineolata*, the prevalent ground beetle, *Amara* sp., and the subprevalent tenebrionid beetle, *Eleodes opaca* (Fig. 22). At the estival peak *Dorymyrmex pyramicus* contributed 65.1% of the ant population and 37.9% of the total population. In the two-week period following this species' numbers fell to nearly nil, but the ground surface ant population was bolstered by a sudden increase of *Crematogaster lineolata* which produced its major peak in this period; *C. lineolata* also contributed materially to the lesser, autumnal peak.

These two species of ants show some interesting stratal relationships. *Crematogaster lineolata* was regularly taken in the sweep collections in the herb stratum of the true prairie subsere, in both day and night samplings. In contrast *Dorymyrmex pyramicus* was never taken in the herbs. The carabid and tenebrionid beetles, *Amara* sp. and *Eleodes opaca*, show comparable stratal relationship. *Amara* was taken frequently in soil and litter samples and in considerable numbers in pitfall collections during the estival aspect in subseral true prairie, but was never found in the sweep net collections in the herb stratum. *Eleodes opaca* was at no time secured by sweeping the herbs during the day but appeared in noteworthy numbers in the night sweeps.

Inasmuch as most studies of stratification and inter-stratal movement of invertebrate animals have been made in forest habitats, a consideration of these phenomena in the postclimax shrub station is of special interest here. Such vertical behavior is more easily recognized and measured in this essentially forest margin habitat than in the grassland, the plant cover being higher and thereby offering deeper and more divergent, if not more strata as regards both biotic factors and physical factors as they are modified by the vegetation. Comparable and simultaneous sampling methods in the herb and shrub strata of this station offer special scrutiny of these two strata.

Considered as an entity the postclimax shrub community produced two relatively enormous population peaks in its aerial strata in 1938, the first a vernal peak in the shrub stratum, the second a late autumnal peak in the herb stratum (Figs. 25, 27). The early autumnal high which occurred in the ground surface population in the following year (Fig. 28) may or may not be related to the autumnal high of the herb stratum; the six weeks difference in time of occurrence (as the findings for the two consecutive years are compared) may have been actual, or the product of a disturbed phenology and aspection under the influence of drought. A second marked peak in the shrub stratum, contributed to in considerable measure by the homopteran

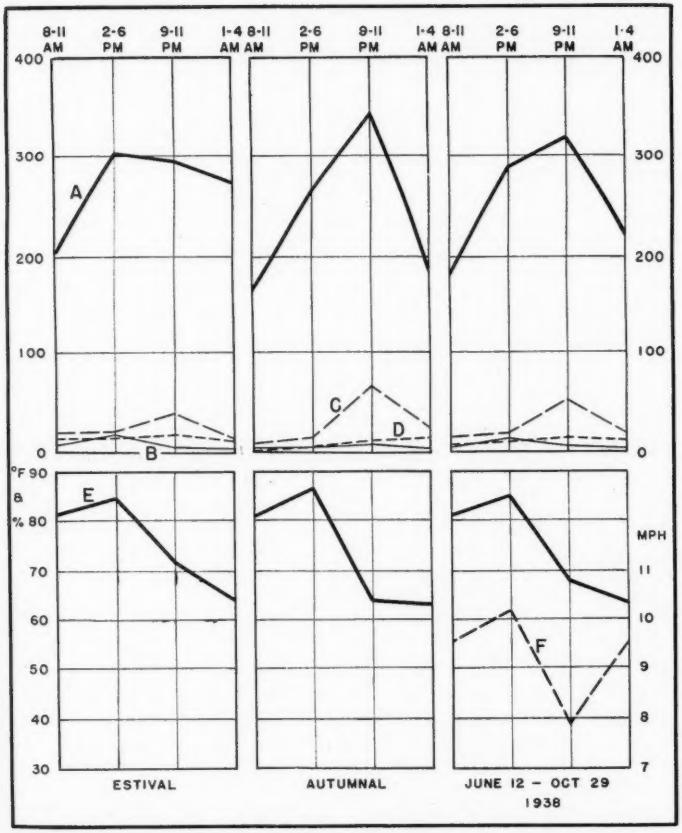


Fig. 32.—Diurnal and nocturnal values of invertebrate populations and temperature in the herb stratum of postclimax tall grass, and of wind at Lincoln, Nebraska, expressed as means for the periods indicated. Total population (line A); *Balclutha abdominalis*, a leafhopper (line B); *Delphacodes* sp., a leafhopper (line C); *Melanoplus bivittatus*, a grasshopper (line D); Temperature °F. (line E); Wind velocity (line F).

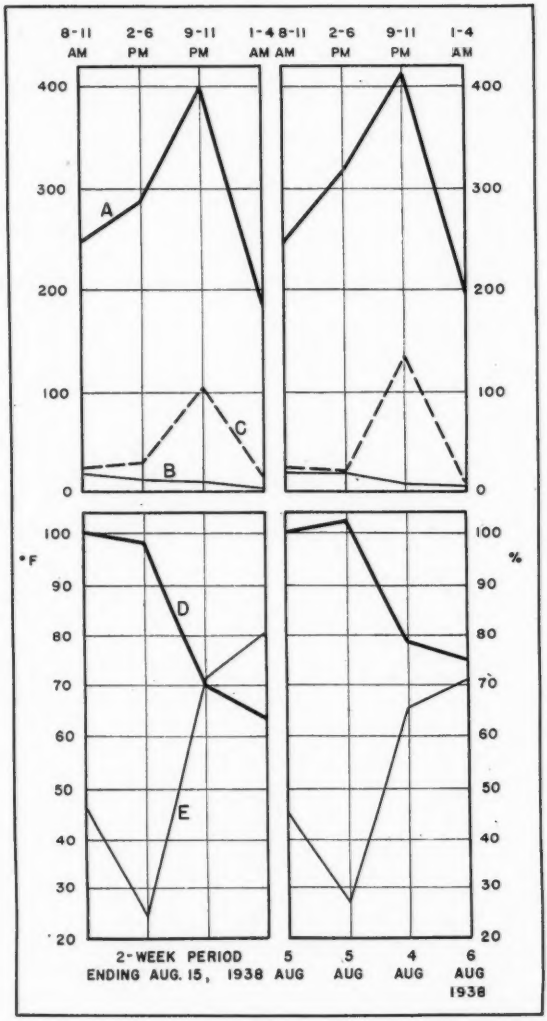


Fig. 33.—Diurnal and nocturnal values of invertebrate populations, temperature, and relative humidity in the herb stratum of postclimax tall grass, expressed as means for the intervals indicated within the two-week period ending August 15, 1938, and as actual values and collection averages within a 31-hour period, August 4 to 6, inclusive, 1938. Total population (line A); *Balclutha abdominalis*, a leafhopper (line B); *Delphacodes* sp., a leafhopper (line C); Temperature (line D); Relative humidity (line E).

Erythroneura sp., appeared at the end of the estival aspect. The first of these two major shrub peaks was coincident with the vernal blooming of wild plum. A rather poorly defined tertiary peak of shrub stratum population was produced principally by many species of flies and micro-hymenoptera six weeks later during the anthesis of the dogwood. Following the late estival peak the total population of the shrub layer as measured in this study fell off rather abruptly, being somewhat bolstered, however, in the latter half of August by *Erythroneura*, the beetle, *Chalcoides fulvicornis*, and the order Diptera. This decline in shrub layer population was coincident with the loss of leaves suffered by *Prunus* and *Cornus* in this situation which may have in part resulted from injury by *Erythroneura*. There is little or no evidence of downward migration into the herb stratum in this instance—the total population of the herb was likewise decreasing. Values for the 12-day period ending September 24, 1938, show the shrub stratum population at zero, and the herb stratum population at the lowest point since late in the vernal aspect. At this point the remarkable autumnal high of the herb stratum begins to form, reaching its zenith in the next four weeks thence to fall off within six weeks to hiemal levels.

The compositions of the peaks in these two aerial strata are interesting. The vernal peak in the shrub stratum coming at the time when *Prunus* was flowering was made up of many species. Even the insect groups contributing most heavily to this high, namely Diptera, Coleoptera, and winged Hymenoptera comprised only 34.3%, 17.7%, and 16.5%, respectively, of the total numbers of invertebrates; the prevalent, *Chalcoides fulvicornis*, a flea beetle, was on the decline and comprised but 15.7% of the peak population. Here is indicated (1) the presence of many species and (2) the formation of a total population peak independent of a single species pattern.

The late autumnal peak in the herb stratum of the same station (a high more than twice the magnitude of the vernal peak in the shrub stratum) was largely the function of populations of Diptera and Homoptera, these orders comprising, respectively, 53.8% and 23.0% of the total population. However, the two prevalents, *Dikraneura abnormis* (Homoptera, Cicadellidae) and *Anoecia graminis* (Homoptera, Aphididae), and the two subprevalents whose population peaks occurred in this period, namely, the flies, *Oscinella coxendix* and *Elachyptera costata*, jointly contributed only 35.9% to the total peak. *Dikraneura abnormis* was in decline; the most abundant fly, *Oscinella coxendix*, comprised but 21.0% of its order and 11.3% of the entire population of the herb stratum. Single species appear to contribute only lightly to the formation of this autumnal peak.

It is of especial significance to note that *Anoecia graminis*, the aphid which as a single species contributed the greatest population values to this peak in the herb stratum of the shrub station, was confined to this stratum and this station. *Dikraneura abnormis*, a cicadellid leafhopper, which had forced a previous lesser peak by forming 32.9% of the total population during the fortnight ending August 29, was likewise confined to this stratum and station, so far as the methods of study ascertained. The leafhopper, *Erythroneura* sp., was taken only in the shrub stratum of this station, and the chrysomelid beetle, *Chalcoides fulvicornis*, was confined to the shrub station and largely to the shrub stratum.

On the surface of the ground under the shrubs the cydnid bug, *Geotomus robustus*, and the dung beetle, *Ataenius cognatus*, were omnipresent through-

out the period of the pitfall studies in that station (May 28 to November 4, 1939); the harvestman, *Leiobunum* sp., was also continuously in evidence until early October. The outstanding autumnal peak in this situation was almost entirely the function of *Geotomus robustus* and *Leiobunum* sp., the bug contributing 69.3% of the total numbers, the phalangid 14.6%—together 83.9% of this total ground surface population as measured. *Geotomus robustus* was taken only in the shrub station in ground surface or litter collections, with the exception of a single specimen taken in the alcohol pitfall in the true prairie subsere during the week ending September 23, 1939.

Certain of these prevalents, representing, to be sure, relatively few species, were apparently subject to vertical limits of distribution in the deciduous shrub habitat. The cydnid bug, *Geotomus robustus,* and the dung beetle, *Ataenius cognatus,* were taken commonly and in considerable numbers in the ground surface collections, sparingly in the litter collections; the harvestman, *Leiobunum,* commonly, and briefly in large numbers, in ground surface collections, in small numbers in the herbs. The leafhopper, *Dikraneura abnormis,* and the aphid, *Anoecia graminis,* were taken only in the herb stratum. *Erythroneura* sp., another leafhopper, was taken solely in the shrub collections, sharing prevalent values here with the flea beetle, *Chalcoides fulvicornis,* which was taken only sparingly in the herb stratum. On the other hand, the ant, *Prenolepis imparis,* was found in important numbers on the surface of the ground, in the herbs, and in the shrub stratum.

Data on daily fluctuations of arthropod numbers in the shrub station are not as complete as desired, but the curves derived show the pattern of daily movements (if the fluctuations in take indicate movements) in the herb stratum to be somewhat different from those in the prairie habitats (Figs. 30, 32, 34). For the June 12 to October 15 period the daily high (mean) occurred in the day A.M. period with the low in the night A.M. This before-dawn low agrees with the grassland pattern; likewise a build-up from day P.M. to night P.M. is similar. But the sudden eruption from the night A.M. daily low to the day A.M. daily high is strikingly different. The temperature-relative humidity pictures are comparable except that in the shrub station (ravine) the night P.M. temperatures dropped faster and humidity values built up faster than in the grassland. This may be a function of the cold air drainage described earlier and a phenomenon known to all who have traveled country roads in rolling country on summer nights. The striking wind velocity differences must also be remembered in this instance.

These curves largely reflect those for the autumnal aspect, data from the estival being incomplete. It will be noted that slight temperature increases are indicated for the night A.M. over the level for the night P.M., and that on the two temperature rises, whether great or small, smaller numbers of invertebrates were taken in the sweep net. In the true prairie subsere, however, the greatest numbers of animals were taken in the night P.M. when temperature values were below those for the day (Fig. 30).

The curve of the herb population in the shrub station (Figs. 34, 35) tends downward (instead of upward as in the prairie station) from a day A.M. high, while the curve of the shrub population is tending upward. This might indicate that the herb stratum was losing its population to the shrub stratum above it during the day, the shrub peak being reached in the day P.M. With the coming of darkness, and its lowering temperature, increasing relative humidity,

and low wind values, the shrub curve tends downward and the herb population shows a marked increase, apparently indicating that the shrub day popu-

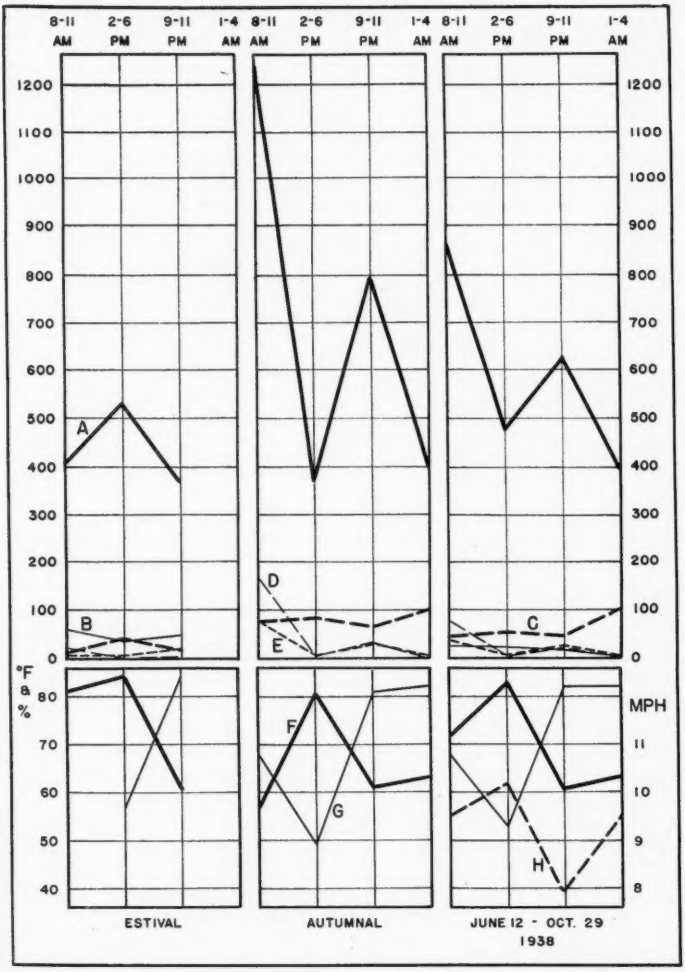


Fig. 34.—Diurnal and nocturnal values of invertebrate populations, temperature, and relative humidity in the herb stratum of postclimax deciduous shrub, and of wind at Lincoln, Nebraska, expressed as means for the periods indicated. Total population (line A); *Balclutha abdominalis*, a leafhopper (line B); *Dikraneura abnormis*, a leafhopper (line C); *Anoecia graminis*, an aphid (line D); *Prenolepis imparis*, an ant (line E); Temperature (line F); Relative humidity (line G); Wind velocity (line H). No 1-4 AM collections in this habitat during the estival period—see Table 32.)

lation is in part gathering in the lower stratum. The night A.M. low for both strata shown by the continued fall of both curves would indicate a telescoping of both populations in the lowest vegetational levels. The seemingly incongruous high in the herb day A.M. population is apparently the result of a returning vertical movement, aerial or epiphytic populations now moving upward somewhat simultaneously toward the maximum vertical spread which is reached in the afternoon when the temperatures are highest, humidity lowest, and wind velocity at its normal daily maximum.

The curves representing daily fluctuations of invertebrates in the two aerial strata studied in the shrub station show strikingly different patterns from those

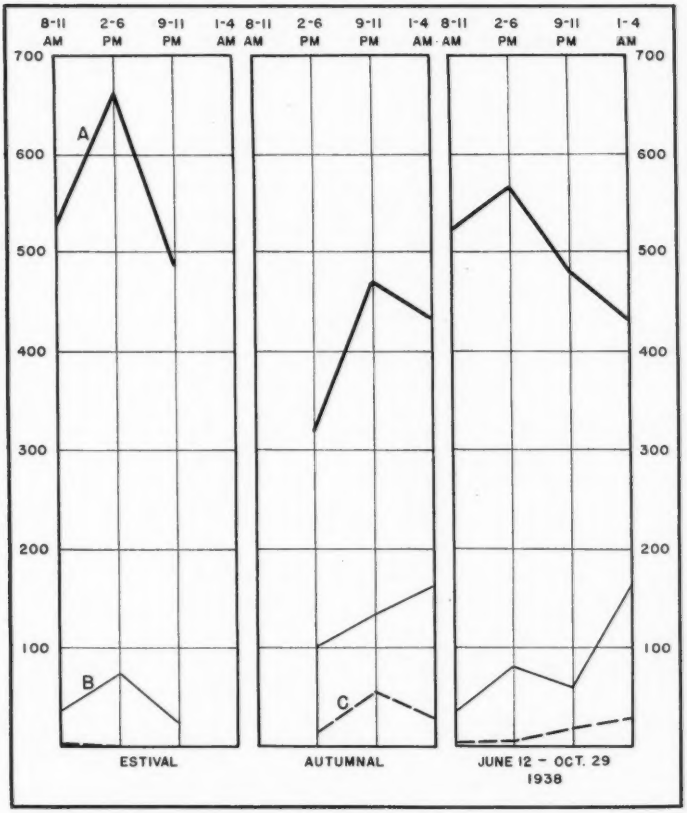


Fig. 35.—Diurnal and nocturnal values of invertebrate populations in the shrub stratum of postclimax deciduous shrub, expressed as average numbers per collection for the intervals indicated. Total population (line A); *Erythroneura* sp., a leafhopper (line B); *Crematogaster lineolata*, an ant (line C). (No. 1-4 AM collections in this habitat during the estival period—see Table 32.)

in the grasslands, but appear to express, in general, the same responses to physical factors.

Accounts of Prevalents

Delphacodes sp. (Tables 27, 29, 33; Figs. 19, 30, 32, 33).—If it is ecologically valid to consider that an invertebrate species can attain prevalence in an aerial or epiphytic stratum during the hiemal aspect, this member of the homopteran family Fulgoridae became the hiemal prevalent in the herb stratum of the drought-disturbed true prairie, where it was taken in every month excepting April and December. However, it should be noted that six sweep collections made in both the tall-grass and subseral true prairie during the winter of 1937-38 yielded no specimens of this form, all of the hiemal specimens being taken during the next winter, 10 out of 14 samples containing *Delphacodes* in the true prairie subsere, and 7 out of 17 producing in the tall grass. Temperature differences were not present to account for this discrepancy. If one of the objectives of this study had been the naming of communities, and data from the second winter only had been available, this hiemal society could have been accorded a name based on an animal that was absent from the society in the previous year.

Delphacodes was confined to the two prairie stations, first appearing in the tall-grass (ravine) herb stratum collections on April 25 (1938), in the prairie subsere (upland) sweeps on May 30. This five-week lag is illustrative of the aspectional sequence shown by ravine and upland sites in early spring, discussed earlier in this paper.

In the true prairie subsere where it occurred in 66.6% of the herb stratum collections and produced 4.8% of the total annual population figure, it showed an abundance peak for the two-week period ending July 18, 1938, its collection average during this interval being 47, and forming 13.3% of the total take (Fig. 19). Its peak of abundance in the tall grass came in the fortnight following, during which time it constituted 16.3% of the total population and averaged 83 specimens per sample.

Balclutha abdominalis (V.D.) (Tables 27, 29, 33; Figs. 19, 20, 30-34).—This cicadellid leafhopper was the most important species taken on the basis of numbers, frequency, and distribution, being the prevernal-vernal, estival, and autumnal prevalent in the herb stratum of subseral true prairie, the estival prevalent in the herb stratum of postclimax tall grass, and the prevernal-vernal prevalent in the herb stratum of postclimax deciduous shrub. Its greatest abundance occurred in the true prairie subsere (Fig. 20), producing here a daytime collection frequency of 69.3% and comprising 17.4% of the total numbers taken. In the tall grass its day collection frequency was 50.8%, its percentage of total numbers taken only 5.8%; under the shrubs it constituted 4.4% of the total take and occurred in 46.0% of the samples.

Balclutha abdominalis was first taken on March 19, 1938 in the postclimax shrub station, and appeared nearly a month later, April 25, in the prairie habitats. It was last collected in the prairie stations on October 29 but lingered awhile under the shrubs, being last taken there on November 11 although no specimens were collected there during the autumnal season. An early hiemal movement of this cicadellid into the shrub habitat may be indicated by these data.

During its period of aerial or epiphytic activity its collection frequency in

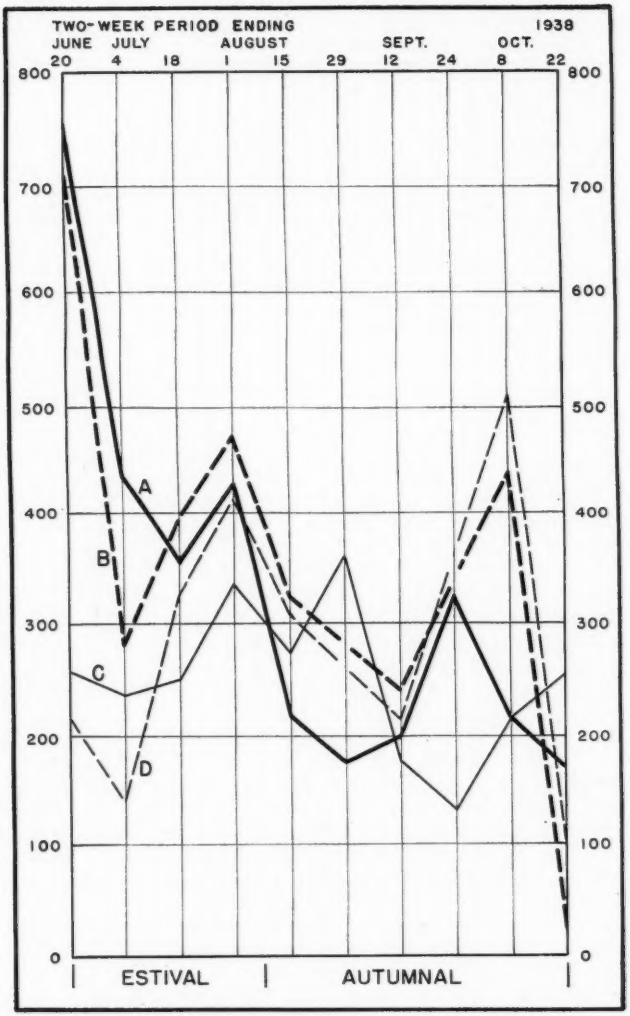


Fig. 36.—Diurnal and nocturnal trends of total populations of invertebrates (arthropods) in the herb stratum of grassland, expressed as average numbers per unit collection (sweeps) per two-week period, June 6 to October 22, 1938. Subseral true prairie: day (line A) and night (line B); Postclimax tall grass: day (line C) and night (line D). (No night collections during the two-week periods ending August 29 and September 24—see Table 32.)

Stations 1, 2, and 3 was 96.3%, 86.1%, and 63.3%, respectively. Its collection frequency in the true prairie subsere and tall grass for the estival aspect was 100%, the average collection numbers for these two stations being 89 and 17, respectively.

Two population peaks were produced in the true prairie subsere by this cicadellid (Figs. 19, 20), the first an estival high for the two-week period ending June 20, 1938, with a collection average of 235 individuals comprising 10.4% of the total population, the second an autumnal peak for the fortnight ending October 8 with a collection average of 113 specimens constituting 52.1% of the total numbers taken in that period. In the two weeks ending July 4 it produced peak values in the two postclimax stations, forming during this interval 29.4% of the herb stratum population in the tall grass with a collection average of 61 and 18.5% of the total herb population in the shrub habitat with a collection average of 77.

Dorymyrmex pyramicus Roger (Tables 27, 29; Figs. 22, 29).—This small ant is common, nesting in the ground and preferring open, sunny spots. The workers feed mainly upon other insects, but are also fond of "honey dew" from aphids. Although found in all kinds of soils, it seems to prefer light, dry soils (Bare, unpublished manuscript and personal communication).

Dorymyrmex pyramicus is chiefly notable here for its almost complete confinement to the upland subseral true prairie as determined by pitfall collections, and its apparently complete absence from the shrub station, a distribution in keeping with Bare's observation that it seems to prefer light, dry soils. It was taken only in ground surface collections, first appearing in them in subseral prairie in the fortnight ending June 17, building up to a rather high peak for the two weeks ending July 15, thence disappearing from the collections following August 26 (Table 29; Figs. 22, 29).

Crematogaster lineolata Say (Tables 27, 29, 33; Figs. 22, 24, 29, 35).—O. S. Bare (unpublished manuscript and personal communication) states that *Crematogaster lineolata* is a very abundant ant in this region, nesting under stones and logs, in dead wood, beneath the bark of trees, and often in the soil. Its food habits vary; it feeds to considerable extent on animal matter, mainly insects, but is also fond of sweets and may often be found attending aphids.

This ant was the autumnal and early hiemal prevalent in the ground surface stratum of subseral true prairie and the estival prevalent in that stratum of postclimax tall grass. It occurred in the herb, litter, and ground surface collections of all three stations and in the shrub layer of Station 3. Dowdy (1947) reports this ant abundant and distributed "through all five strata" in oak-hickory forest. Its numbers were never remarkably great, although its peak of population in the subseral prairie ground surface stratum showed a two-weeks pitfall take of 207 specimens which comprised 48.8% of the total take (Figs. 22, 29). It appeared somewhat earlier and disappeared slightly later in the herb layer collections in the shrub habitat than in the other two stations.

Piesma cinerea Say (Tables 27, 30, 33).—Rather unrestricted in its spatial distribution within the area studied, this tingid bug was the hiemal prevalent in the litter stratum of the two prairie stations. It was important in the hiemal litter collections in all stations, however, and produced its highest values in the shrub habitat where a collection average of 38 individuals accounted for 32.5% of the sample. One of the shrub litter collections in

this period yielded 67 specimens of this bug which was 38.0% of the total number of invertebrates present. This was undoubtedly a massed group of hibernating *Piesma cinerea*, the finding of such aggregations being common in litter samples. The coccinellid beetle, *Hippodamia convergens*, was frequently found in this manner, further exemplifying the spotty distribution of certain hibernating insects.

Piesma cinerea was taken in low though noteworthy numbers in the herb stratum of the two postclimax stations in April and May of 1938, first appearing in the shrub habitat in sweeps made on April 18, in the tall grass on May 2. Its appearance in relatively large numbers in the herb stratum of the tall-grass station was sudden, the May 2 collection taking 67 specimens, the largest number taken in any sample at any time. On this same date a light peak of vernal abundance was evident in shrub station sweeps. The bug's numbers in the herbs of both habitats declined rather quickly, last appearing in the tall-grass sweeps on May 23, in the shrub station on June 12. In this latter site it reappeared in low numbers in mid-October. There are no indications of its whereabouts during the balance of the estival and autumnal periods.

These data seem to indicate, however, a vernal-early estival emergence of hibernating adults of *Piesma cinerea* from hibernacula in the shrub and tall-grass habitats, activity beginning earliest in the shrub station, and a return to these sites in the late autumn—illustrating the horizontal-vertical prehibernation movements pointed out by Weese (1924).

It must be remembered that hibernating individuals of *Piesma cinerea* were also taken in the litter in the upland true prairie subsere. It should further be noted that this bug was taken in the shrub stratum in 25.0% of the collections, albeit in very low numbers.

Fridericia spp. (Tables 27, 30).—Confined to the litter and soil of all stations studied, this little annelid proved to be the prevernal-vernal-estival prevalent in the litter stratum of subseral true prairie and postclimax deciduous shrub and the estival prevalent in the litter of the postclimax tall-grass habitat. Data concerning it are considered quite inadequate here, and it figures but little in this analysis. However, it is noteworthy that this genus of enchytraeid worm exhibited peaks of abundance in the litter stratum of the two postclimax vegetational units—in the shrub station for the two weeks ending April 5, 1938, where it comprised 55.1% of the litter population as sampled and averaged 117 individuals per collection (square foot), and in the tall-grass station from June 20 to July 4 where a unit collection average of 47 specimens comprised 88.5% of the total number of invertebrates taken.

It occurred in winter samples of litter in these two stations, but with much less regularity than during the warmer seasons.

Amara sp. (Tables 27, 29, 30; Fig. 22).—The carabid, *Amara* sp., was taken in those strata which would be expected of a ground beetle—namely, the soil, the litter, and the ground surface. It occurred in all three stations, but principally in the grassland stations. Its most important numbers appeared in the soil stratum of the tall grass where it comprised 44.0% of the total population as sampled, occurring in 68.4% of the collections; here it was the annual prevalent. It likewise proved to be the annual prevalent in the soil stratum of the true prairie subsere, where it was also the autumnal prevalent in the litter stratum and the prevernal-vernal prevalent of the ground surface stratum. Its only noteworthy peak of abundance occurred in the ground sur-

face stratum of the subseral prairie station during the fortnight ending June 17, 1939 (Fig. 22). In this cumulative two-weeks collection this ground beetle formed 14.9% of the total take. It first appeared in the pitfall collections in this site between April 22 and May 6 and was last taken in the collection for July 29 to August 12. Its litter collection frequency was greatest in the tall-grass station where it was taken in greatest abundance from mid-April to early July. Its soil values were also highest in the tall grass, producing a collection frequency of 68.4% and 44.0% of the total population secured.

Melanoplus bivittatus (Say) (Tables 27, 30, 33; Figs. 23, 32).—The two-lined locust is listed by Peairs (1940) among what he terms the five important species of grasshoppers which are widespread as well as destructive. This conspicuous member of the prairie fauna overwinters in the egg stage in the ground, hatches in the spring, and appears as adults in midsummer. It continues feeding until cold weather kills it. Grass is the normal food for grasshoppers, but this species will feed on nearly any kind of vegetation. Dry conditions probably favor hatching.

Remarks on grasshoppers as a group or as species in this study should be prefaced with the note that it is probable that sweep collection records do not furnish data which truly reflect grasshopper populations. The life habits, especially the alertness and escape responses of grasshoppers are thought to make it impossible to take completely reliable sweep net samples of grasshopper populations in daylight and in warm weather. It is felt that night sweeps might give a more accurate picture of grasshopper numbers, presuming, of course, that darkness covering the activities of the investigator leaves the grasshopper comparatively little disturbed until taken.

Melanoplus bivittatus made its earliest appearance as nymphs in the southwesterly sloping (ravine) tall-grass station, in a sample of the herb populations taken on April 25, 1938. A week later the species was present in all stations, but produced its greatest numbers in the tall-grass habitat, where it appeared in 49.2% of all day sweep samples and comprised 5.7% of the entire (annual) population. It showed peaks of abundance in both postclimax stations for the two weeks ending May 23; in the tall grass its collection average was 67 during this fortnight and it made up 19.9% of the population (Fig. 23); in the deciduous shrub station it yielded 30 specimens per collection and furnished 6.8% of total numbers.

Melanoplus bivittatus was taken in 16.6% of the daytime collections in the shrub stratum, but comprised only 0.14% of the specimens taken. The species apparently disappeared first in the true prairie subsere, although mowing undoubtedly confused the picture here, and was last taken in the postclimax vegetation in mid-October.

Lygus pratensis (Linn.) (Tables 27, 30, 33; Fig. 23).—After wintering in trash and debris of all kinds, adults of *Lygus pratensis* appear with the first warm days of spring. Older nymphs and eggs may also survive winter. After their spring emergence bugs of this species feed for awhile in grassy fields and on weeds. There may be several generations per year; in the autumn the life cycle occupies 30-35 days (in Missouri), probably less in the earlier, warmer part of the year (Herrick 1925, Fernald and Shepard 1942).

Blake (1926) found the tarnished plant bug appearing "in considerable but varying numbers throughout" the period of his study on the animal ecol-

ogy of deciduous forest in winter in Illinois. He found it in increasing numbers on the shrub and herb strata during the fall; it then disappeared from these epiphytic strata and "became abundant in the leaf stratum" (on forest floor) . . . indicating "an inward migration from the forest border, followed by a downward migration into the leaves, similar to that described by Weese for several species of forest-border beetles in this same habitat." Adams (1941) likewise found *Lygus pratensis* to be a "hibernating species which occurred in the ground stratum during the winter." Both authors report it on the herbs and bare shrubs on "warm" winter days.

The tarnished plant bug was taken in all of the habitats studied, its greatest numbers occurring in the tall-grass and shrub stations where its annual collection frequencies were 31.1% and 36.0% respectively, comprising 14.0% and 15.1% of the respective populations. Its classic late autumnal and early hiemal behavior in the herb stratum of hibernation cover was evident in both postclimax stations. In the tall-grass habitat it showed such high values that it became the autumnal prevalent of the herb stratum in that station (Fig. 23). There, during the two-week period ending October 22 its average sweep sample number was 80, making up 31.3% of the total specimens taken. One collection during that period, made during the forenoon of October 15, contained 232 specimens of *Lygus pratensis,* a value 60.6% of the total sample. Its autumnal peak in the herb stratum of the shrub habitat occurred two weeks later than that for the tall grass, in both 1937 and 1938. This possibly suggests a movement from tall-grass situations to shrubby cover following an earlier concentration in the tall grass, or a movement of at least a part of the tall-grass concentration. This is further suggested by the fact that collections from the litter stratum taken throughout the hiemal period showed *Lygus pratensis* to be hibernating in that stratum in both postclimax stations, but in much greater abundance in the shrub area. Only 3.3% of the litter collections in the tall grass produced bugs of this species, while a third of those from under the shrubs contained the species. The bug was present in low numbers in the grassland stations throughout the prevernal-vernal, estival, and early autumnal aspects, but in low numbers infrequently taken. During the month of May in 1938, large numbers of hemipteran nymphs were present in the shrub station; they may have been and probably were nymphs of *Lygus pratensis.* Unfortunately, they were not reared to adults or identified as juveniles.

Prenolepis imparis (Say) (Tables 27, 31, 33; Figs. 24, 26, 28, 29, 34).—The ant, *Prenolepis imparis,* was the early hiemal prevalent in the ground surface stratum of postclimax tall grass and deciduous shrub, as determined by pitfall studies during 1939. During the two weeks ending October 7 this species exhibited a population peak constituting 30.5% of the total ground surface population values for the same period; its annual collection frequency in this site was 45.8% and it comprised 5.5% of the annual population (Fig. 29). In the tall grass its peak of abundance occurred in the following fortnight with an average colletcion value of 15, making up 15.8% of all specimens taken. It likewise produced a peak of abundance in the subseral true prairie, during the fortnight ending July 15 with a take average of 21 and a total population percentage of 2.7. Despite these lower values for the grassland stations during the period of its population peak, its annual collection frequencies in these habitats exceeded those for the shrub, being 60.0% in

the upland prairie and 66.6% in the tall grass, its proportion of total populations in these two stations 3.8% and 5.1%, respectively.

Prenolepis imparis, according to Bare (unpublished manuscript and personal communication) is a very common ant throughout eastern Nebraska, where it nests in the ground, preferring heavy clay soils in moist locations, particularly in woodlands. It is active mainly in moist, cool weather, inactive through the hot, dry portion of the summer. The workers attend aphids and feed on "honey dew."

The cosmopolitan horizontal distribution of *Prenolepis imparis* in the prairie tract studied has already been indicated; it showed deep distribution vertically, as well. Dowdy (1947) found *P. imparis* one of the most abundant species of ants in oak-hickory forest, and distributed "through all five strata." It was present in 29.2% of the shrub stratum collections, but formed only 1.8% of the total population taken. It showed a peak of abundance in this stratum for the two-week period ending May 9, 1938, averaging 40 specimens per collection and making up 3.5% of the total numbers. Under the shrubs it was showing a peak in the herb stratum for the same period, averaging 30 specimens per sample here and yielding 10.0% of the total take.

A second peak of abundance in the herb stratum of the shrub station which occurred in the fortnight ending October 22 sents its collection average up to 120; its total population proportion was, however, down to 5.0%. It is of special interest to note that the aphid, *Anoecia graminis,* produced its population peak in this same situation, to which it was confined, and in the same period (Fig. 26). The "tending" relationship with *Anoecia graminis* is further illustrated in the daily curves for the two species as presented in Figure 34, those for the autumnal period being especially clear.

Prenolepis imparis was taken in 100 0% of the night collections made in the herb stratum of the shrub station (June 18 to October 21, 1938), yet yielded only 3.6% of the total take. Its night collection numbers showed a peak corresponding with that for day collections for the two weeks ending October 22, its collection average being less than that for the day sweeps, but comprising slightly more of the total population. Its night population in the herb stratum also showed a high for the fortnight ending June 20; *Anoecia graminis* was also present in the herbs at this time but in much smaller numbers than at its remarkable late autumnal peak (Fig. 26).

Blissus leucopterus (Tables 27, 30, 33).—The chinch bug has been labeled as one of the most injurious insect pests of cereal crops in the United States (Swenk and Tate 1941:3). That this important crop pest maintains itself from year to year in grassland has been pointed out by Osborn (1939:174), being also injurious to grasses (Herrick 1925:366), feeding on all the grasses (Fernald and Shepard 1942). Although it hibernates in many situations, such as "leaves and litter under borders of woodlots," its favorite and most successful wintering place in the plains states is in the dense tufts of bunch grasses, especially the blue stems (Whelan 1927, Swenk and Tate 1941:5).

Emergence of the hibernating population of chinch bugs is gradual, and the spring dispersal to small grains and grasses usually begins when temperatures attain 70°F. or more for a few days in succession. In Nebraska this usually takes place in early April through May. Egg deposition is irregular also, taking place at or just below the surface of the ground from late April

to late June. The first generation appears in about 45 days, and in the middlewest young of a second generation appear in August and early September. *Blissus leucopterus* is particularly affected by weather conditions, apparently being favored by dry weather. Heavy spring rains during the hatching period are said to be suppressive (Herrick 1925:320, Osborn 1939:175, Swenk and Tate 1941).

Blissus leucopterus, reported as an original inhabitant of true prairie (Clements and Shelford 1939:275), was the prevernal-vernal and hiemal prevalent in the litter of postclimax tall grass. In this habitat it was taken in 46.7% of all litter collections. In eight collections made here from May 9 to October 8, inclusive, a period encompassing the entire estival aspect, no chinch bugs were found. Out of 18 prevernal-vernal, autumnal, and hiemal samples from the litter stratum of the tall-grass habitat, 14 contained chinch bugs, the numbers ranging from 1 to 102 per square foot sample. This bug was also taken with approximately the same frequency in litter collections under the shrubs but averaged less than one-third as many individuals per collection. Its autumnal appearance in the litter stratum was discovered in collections made on October 15 in both ravine stations. Out of 23 prevernal-vernal, estival, and autumnal collections of litter in the true prairie subsere, only one contained chinch bugs, and that only two specimens.

Sweep collections took chinch bugs in the herb layer only in March, April, May, late September, and October, and these in greatest abundance in the tall-grass habitat. This suggests its virtual absence from the prairie tract during the estival and early autumnal aspects.

Chalcoides fulvicornis (Fabr.) (Tables 27, 31, 33; Fig. 27).—This flea beetle was the prevernal-vernal prevalent in the shrub stratum of postclimax deciduous shrub. Occurring in 79.2% of all shrub layer collections, it attained its peak during the fortnight ending April 25, averaging 185 specimens per unit sample and comprising 23.5% of the total numbers. It was also taken in the herbs of this station but in numbers so low as to suggest that it was in this stratum accidentally.

Erythroneura sp. (Tables 27, 31, 33; Figs. 27, 35).—Population values determined for this leafhopper show it to have been the estival-autumnal prevalent in the shrub stratum of the postclimax deciduous shrub station. In this situation it appeared in 79.2% of all day time collections, and in 100.0% of all night collections. It made up 8.3% of the day time population, 22.4% of the night population. In the fortnight ending August 1, 1938, *Erythroneura* produced its population peak, showing 175 specimens per unit daytime collection and comprising 22.6% of the total population. In the following two weeks it showed a peak in the night sweeps, averaging somewhat fewer specimens per collection, 155, but forming a greater percentage of the animals present, 33.3%. These data suggest that either (1) in the event this invertebrate population thinned out of the shrub layer under the impact of night conditions, the population of *Erythroneura* was less affected, or (2) night conditions increased the susceptibility of this leafhopper to capture by the sweep net to a greater degree than it did the remainder of the animals present. However, autumnal averages show the night P.M. and night A.M. collection values of *Erythroneura* in ascendancy, and an upward movement into the shrub stratum during the cooler and more moist portion of the daily cycle is suggested (Table 33; Fig. 35).

Peairs (1941) lists six species of *Erythroneura* as grape leafhoppers. "There seems to be little important difference in the biology of the various species," Peairs says. They winter as adults, feed on plants other than grape before grape foliage becomes plentiful, and produce two broods per season. Adults of the second brood go into hibernation when forced by lack of food and occurrence of frosts. Early season rainfall seems to be unfavorable to these leafhoppers. Defoliation of infested trees may be several weeks earlier than that of trees free of the insects.

Adams (1941) found three species of *Erythroneura* the "most common species of leafhoppers in the tree stratum" in the "young elm-maple stage of a deciduous forest climax" in Tennessee, where they were "occasionally taken from the herb and shrub strata at noon and in the late afternoon" in small numbers. Blake (1926:95[459]) listed *Erythroneura obliqua* as one of five "predominants from the summer shrub societies" of deciduous forest in Illinois.

In the postclimax deciduous shrub station *Erythroneura* sp. was taken only in the shrub stratum.

Dikraneura abnormis (Walsh) (Tables 27, 31, 33; Figs. 25, 26, 34).—The distribution of this autumnal prevalent in the herb stratum of postclimax deciduous shrub illustrates rather sharply defined habitat preference. It was taken only in collections from that situation, in which it was prevalent. Present in these sweeps from June 12 to November 11, 1938, it apparently produced two peaks of abundance—the first in the two-week period ending August 29 when it formed 31.2% of the population of the herb stratum, the second and lesser peak for the two weeks ending October 8 when it comprised 10.2% of the numbers collected.

Anoecia graminis Gillette and Palmer (Tables 27, 31, 33; Figs. 25, 26, 34).—Making its autumnal appearance in the herb stratum of the postclimax shrub habitat in sweeps made on September 18, 1938, this aphid produced its population peak by the middle of the fortnight ending October 22, and attained the rank of early hiemal prevalent in this society. It shared confinement to this habitat with the leafhopper, *Dikraneura abnormis,* and was responsible for 12.4% of the dramatic total population peak in this stratum and station for the two-week period ending October 22 (Fig. 25).

Patch (1938:60) lists *Anoecia graminis* as feeding on grasses of the genus *Hordeum.* Steiger (1930:188) lists two species of *Hordeum* growing on "disturbed areas" within this prairie tract. Whether this genus of grasses was present among the herbaceous growth of the shrub station in 1938 is not known. Osborn (1939:165) states that *Anoecia corni* (Fabr.) and *A. querci* (Fitch) alternate between grass and dogwood, being found on the latter in the autumn, and that *A. querci* is largely dependent upon ants. Indications of this aphid's relationship to ants as shown by this study have been reviewed in the account of the ant, *Prenolepis imparis* (Fig. 34).

Geotomus robustus (Uhler) (Tables 27, 31; Fig. 28).—According to Comstock (1940) members of the hemipteran family Cydnidae burrow in sandy places, or are found on the surface of the ground under sticks and stones, or at the roots of grass or other herbage.

This bug was almost wholly confined to the shrub habitat where it was taken in soil, litter, and ground surface collections. In the latter stratum it was present in 76.0% of the collections, comprised 33.7% of the total number

of invertebrates taken, and during the two weeks ending September 9, 1939, appeared in such numbers as to force a striking population peak (Fig. 28), 470 specimens comprising 69.3% of the total two-week take. Its numbers in the soil built up perceptibly toward late autumn. It thus became the autumnal prevalent in the soil and ground surface strata of postclimax deciduous shrub.

Also noteworthy is the complete absence of this burrowing bug from the pitfall collections in the shrub habitat during the two weeks ending July 22, before which it declined rather steadily from its early summer level, and following which it built up to its remarkable autumnal high.

Leiobunum sp. (Tables 27, 31; Fig. 28).—The harvestman, identified here only to genus but apparently conspecific, showed two periods of marked abundance in the ground surface stratum of postclimax deciduous shrub where it was the estival prevalent. Although the phalangid was taken in 75.0% of the pitfall collections in this situation, both highs had the appearance of eruptions. During the week ending July 8, 1939, a single specimen was taken in the week-long gather of the alcohol pitfall; in the following week 98 were collected. In similar manner, no specimens were taken during the week ending August 19, 7 were taken in the next, and 117 in the next, ending September 2. This seemingly eruptive behavior may have been more apparent than real due to the nature of the pitfall, which is subject to appraisal in another part of this paper. Very small numbers of this arachnid were taken in the pitfall in the tall-grass station.

Ataenius cognatus Lec. (Tables 27, 31; Fig. 28).—Confined to the postclimax deciduous shrub habitat, this dung beetle was the hiemal prevalent in the soil stratum of that station, its litter values being negligible. The little scarab's presence and activity under the shrubs throughout the vernal, estival, and autumnal aspects was evidenced by its frequency of 80.0% in the ground surface (pitfall, 1939) collections in which it comprised 10.1% of the numbers taken. In the collection for the two-week period ending August 12 its population peak was realized, a take of 163 comprising 85.3% of the beetle population and 59.9% of the total.

Discussion

The horizontal distribution of physical environmental factors through the three habitat complexes studied, *viz.*, upland true prairie (in subsere due to recurrent drought), postclimax tall grass, and postclimax deciduous shrub, was apparently somewhat comparable to their vertical distribution within the shrub community. These measurable factors would not, of course, present a graded horizontal series such as those pointed out by several workers for the vertical gradients of physical conditions in forests. Although the data presented here regarding evaporation, an environmental force now established as a fairly reliable index of the combined operation of other physical factors of the atmosphere, are inadequate, measurements of this force in the three vegetational units point to this analogy. Of the three habitats, the upland true prairie exerted the greatest evaporation stress upon its herb inhabitants, the deciduous shrub the least, but the inhabitants of the shrub stratum in the latter community were subjected to rates which approached those in the herb layer of the prairie. The analogy is especially clear when the grouping of wind velocity values is considered, this environmental factor and that of evaporation apparently being closely related. The picture of physical conditions

in the soil is somewhat less conclusive, yet even in this stratum the differences show a discernibly consistent pattern of distribution through the three habitats. Because of the agreement of life form of the vegetation in the upland true prairie and the included areas of postclimax tall-grass, conditions in these two habitats might be expected to approach each other rather closely, with both at considerable variance with those of the shrub area. This is not always shown, however, especially as regards soil temperature values and wind velocities. Indeed, individual factors exhibited gradients of their own, presenting a complexity of physical conditions which can be thoroughly understood only after measurements of micro-climatic phenomena more detailed and minute than were carried out in this investigation have been made.

The faunal gradient, if the distribution of the invertebrates through these three habitats may be so characterized, was probably in part correlative to this pattern of environmental factors, but due to inter-specific relationships of the animal species, would be less susceptible to analysis. Comparative analysis has disclosed that the communities of invertebrates occupying these three vegetational complexes showed recognizably different though related structure. The population patterns of subseral true prairie and postclimax tall grass, whether considered quantitatively or qualitatively or on the basis of seasons, strata, or daily fluctuations, showed the closest relationship; those of the postclimax deciduous shrub were markedly different from either of the grassland habitats, although certainly related to them. This suggests that the life form of the vegetation, dominating the habitat, is of primary importance in determining the animal communities; the closer relationship of the grass habitats would, of course, be expected. Blake (1926:95-96[459-460]), in his comparison of animal communities of coniferous and deciduous forests, concluded that ecologically it was "the forest cover, that is, the biotic association as a whole," that was "the determining factor for the presence of a typical forest animal community"—that the "nature of the trees" was of secondary importance. The postclimax deciduous shrub habitat studied here closely approaches forest margin conditions although geographically at some distance from deciduous forest as such; the animal communities of the shrub station appear more closely related to deciduous forest communities than to those of the contacting and surrounding grassland. This picture strongly suggests the important bearing of biotic differences (or similarities) of habitats upon horizontal distribution of animals, acting in combination with, but somewhat precedent over the differences (or similarities) in physical factors. Because of topography and farming operations shrub areas such as this are often discontinuous and without connection with the deciduous forests of stream valleys; they present islands of forest margin communities that are interesting ecologically and readily subject to detailed investigations.

In the ground surface stratum ants were precedent (on the basis of numbers) in the two grassland stations, while Hemiptera ranked first in the shrub habitat. Coleoptera maintained a close second in all three situations. The two prairie habitats were characterized in the ground surface stratum by (1) the same two insect groups, namely the order Coleoptera and the family Formicidae, (2) prevalents and subprevalents in the same insect family, namely Carabidae and (3) by the prevalent ant, *Crematogaster lineolata*. Beetles and ants were prominent, though less so, in the shrub station. Species of beetles which showed prevalent and subprevalent values at the ground surface

in the shrub station and the upland prairie represented families of little or no prominence in the tall grass. Distribution of animals and the consequent variation in community structure are, of course, the result of responses to a maze of environmental factors which operate in an effort to satisfy many and changing physiological needs—a complex phenomenon that is reflected in *habitat preference*. Probably more reliable than group differences in this comparison of structure are the habitat choices evidenced by certain species, that is, degree of faunal relationships of the three habitats is probably best expressed by species distribution. For example, the beetle, *Pachybrachys litigiosus*, was an estival subprevalent in both of the grassland stations, but was at all times absent in the shrub complex. The scarabaeid, *Ataenius cognatus*, was confined to the soil and ground surface strata of the shrub area, and the cicadellid, *Erythroneura* sp., was taken in no other sweeps than those made in the shrub stratum of that station. These latter two illustrate, as well, the integrity of stratal societies. On the other hand, *Balclutha abdominalis* was the estival prevalent in the herb stratum of all three stations. A comparison of the distribution of prevalence shown by the 18 prevalent species is interesting in this connection: Two prevalents prevailed in only Station 1, three in only Station 2, three in only Stations 1 and 2, one in only Stations 2 and 3, two in all three stations, and *seven* in only Station 3. These habitat relationships of the prevalents further indicate the faunal correlation of the two grassland stations, and will be considered somewhat further in discussion of prevalents. The greater diversity of animal population structure in the shrub habitat suggested here is probably in part due to the greater internal diversity of habitat, as suggested by Dowdy (1944a:220).

The structural differences in invertebrate communities in the three habitats studied are reflected in the relative rankings attained by major groups within the habitats. The Homoptera, the most abundant group (insect order) found in the aerial strata (as determined on the basis of day sweep collections), composed 33% of the invertebrate population of the herb stratum in the true prairie, an order population 15% greater than that of the second-ranking Coleoptera. In the herb stratum of the postclimax areas, however, the Homoptera were numerically subordinate to the Diptera, and in the shrub stratum, to both Diptera and the winged Hymenoptera. Diptera in first rank in the postclimax stations was relegated to fourth rank in the upland true prairie, with the winged Hymenoptera taking relatively low rank in all societies other than the shrub. The population values of Coleoptera approached each other in the herb of true prairie and the shrub stratum of the shrub complex, tending toward a common but much lower value in the herb stratum of the tall-grass and shrub stations. These are hard-bodied insects and are considered as less affected by evaporation stress than such forms as the Diptera and Homoptera. The Orthoptera showed more striking values, ranking third in both the true prairie and the tall-grass areas, i.e., possessing approximately equal population values in the two grassland communities, while attaining rather low rank in both epiphytic strata of the shrub complex.

Shackleford (1934) has mentioned "the integrity of the seasonal societies" as a striking feature in mixed prairie populations, stating that "no forms were abundant throughout several consecutive seasonal societies." This study has borne out that conclusion, although it was found that certain species, such as *Balclutha abdominalis* showed population peaks in consecutive seasons and

tended to characterize the populations of those two seasons. The combination of abundant species characteristic of one season did not carry over into a following aspect, however, the faunistic composition appearing to change continuously and at times at a rate discernible from day to day. This would be expected, of course, in view of the known variance in emergence and maturity characteristics of insects.

Expression of the prevernal aspect faunistically preceded its expression floristically. Prevernal activity of invertebrates above the surface of the soil began in the shrub community well in advance of that in the other two communities. Such aerial and epiphytic activity, even in the hiemal aspect, appeared generally to be initiated when ascending temperatures reached about 40°F., and was indulged in by relatively very few species.

Definite peaks of total populations occurred in all communities, those of the aerial and ground surface strata being most convincing, possibly because of more reliable collecting methods in these strata. Populations of single species, relatively few in number, appeared largely responsible for population peaks in their respective orders, and contributed in considerable proportion to total population peaks. This relationship has been brought out in earlier community studies. In some instances, group (order) population peaks and, in turn, total population peaks were forced by single species (prevalent and subprevalent) populations. In the herb stratum of subseral true prairie Homoptera and Coleoptera attained their annual (estival) peaks simultaneously. Both the herb and ground surface strata in this station produced estival peaks of population, although in this study the two strata were studied in different years and the chronological relationships of the peaks are not clear. Prevernal-vernal and estival population peaks of certain arthropods were coincident with periods of anthesis of certain plants or groups of plants. Autumnal peaks of total abundance in the herb and ground surface strata, of much greater magnitude than any other highs in their respective strata, were produced in the postclimax deciduous shrub habitat.

The spectacular autumnal highs in the shrub station might indicate an inward and downward movement of grassland species showing pre-hibernation activity. This cannot be considered categorical, however, since the ground surface peaks, as determined in this study, were forced almost exclusively by two species largely confined to this situation. The picture of the autumnal high in the herb stratum is not so clear, but likewise appears to be in considerable measure the function of endemic (although many) species, especially flies. The "inward and downward" movement of arthropods seeking hibernacula, pointed out by Weese (1924) and Blake (1926), did occur, however, most convincingly evidenced by three species of Hemiptera, in both postclimax tall grass and deciduous shrub.

Population peaks may or may not reflect maturity. According to Dr. Martin Muma, Citrus Experiment Station, Lake Alfred, Florida, bugs of the family Nabidae, for example, cannot be swept in any appreciable numbers while still nymphal, but seem to erupt at maturity in a given vegetational unit. Unfortunately, no maturity studies were made in this investigation.

Just as a species tends to have a center of abundance in its horizontal distribution, so its population values will tend to remain highest at its stratal optimum, thinning out above and below the optimum. The dimensions of stratal limits are probably not identical for any two species. Thus, in any

given habitat, there may be many degrees of overlapping by many species. Stratal limits, dictated by the habitat requirements of the species, the general meteorological conditions, the vegetation, and the time of day, may be shallow at one time, deep at another. So may the vertical distribution or layering of the animal fluctuate. A species with deep distribution may occur commonly in two or more levels that have been arbitrarily selected for study and may, thereby, be pointed out as occupying more than one stratum. Arbitrary aerial strata primarily reflect the apparent and well defined layering of vegetation; the gradient factors of the atmosphere, measurable but usually without definite limits, are secondary in determining choice of strata to be examined. It is further conceivable that some species of invertebrates might be distributed through all of the strata chosen, named, and studied as expedience demanded, appearing thereby to conform to no stratal organization as conceived by the investigators.

Stratification of physical factors is precedent over stratification of animals, i.e., vertical distribution of physical environmental factors is not dependent upon animal distribution, at least not directly. The stratal organization of a biota is, on the other hand, in part a response to the vertical gradients of such forces as light, wind, temperature, humidity, and the comprehensive factor, evaporating power of the air—"in part" because such response to physical factors produces a stratification of biological factors which, in turn, exert pressures on and lead to further stratification of other members of the community. These biological pressures are exerted through the requirements for food, shelter, and reproductive activity. Invertebrate animals feeding as adults on, through the surface of, or within roots, stems, leaves, flowers, or fruits become stratified according to their needs just as those biological sources of food are stratified. Blake (1926:65[429]) has pointed out that "a very large number of phytophaga indicate by their vertical distribution that the stratum in which they are found is determined by the presence of the host plant." These same animals may require different sets of conditions at different stages of their life histories, or, as adults, while they are quiescent, resulting in a regrouped but nevertheless defined stratal distribution. Physical factors must remain within certain limits to allow an organism or a group of organisms to successfully respond to the biological factors in a given habitat. Physical shifts may occur beyond these limits forcing still other regroupings that ignore biological pressures. It becomes more nearly accurate to state, therefore, that stratification of both environmental forces and invertebrate animals exists subject to continuous fluctuations of both limits and composition. The very dynamics of stratal distribution may be verification rather than refutation of the concept of such community organization.

Evidence of (1) stratal choice by groups and by species, so well defined in such species as *Chalcoides fulvicornis* and *Anoecia graminis* as to result in virtual stratal confinement, and (2) stratal shifts in physical factors and coincident shifts of groups or species of animals have been pointed out. The role of biological factors in determining stratal distribution is illustrated by the presence of *Chalcoides fulvicornis* almost exclusively in the shrub stratum during anthesis of the wild plum. That biological factors may shift with a daily rhythm is illustrated by the *Prenolepis imparis-Anoecia graminis* relationship. It is not known in this instance, however, which insect is primarily responsible for the shift; the relationship of physical factors to the movement is even more obscure.

Carpenter (1935) has reviewed the few studies which up to that time had been directed toward daily fluctuations of invertebrate populations in prairie-forest ecotone, pointing out the general conclusion that "periodic fluctuations in insect populations take place throughout the several periods of the day much as they do from season to season and year to year." "The importance of daily cycles is appreciated," Carpenter states, "when it is recalled that fluctuations of all kinds play a tremendous role in food chain relationships." Davidson and Shackleford (1929) studied this problem during the vernal aspect in a central Oklahoma prairie.

Adams (1941:214) concluded "that the animals of the forest are on the whole stratified" and that "while there was some diurnal movement from strata to strata on the part of some species, on the whole this was negligible."

Measurable daily fluctuations of total populations of invertebrates occurred in the herb and shrub strata as considered in this study. These population fluctuations appeared coincident with fluctuations in physical factors of the environment as measured, principally temperature of the air, relative humidity, and wind velocity, and were expressed both quantitatively and qualitatively. The behavior of prevalent and subprevalent species presents some evidence of qualitative changes in the invertebrate groupings within the daily cycle.

Seasonal changes in the structure of the invertebrate population in any given stratum, are inevitable under the influence of such phenomena as emergence, anthesis, breeding requirements, and death. For example, in the shrub stratum during the flowering period of *Prunus*, Diptera composed 34% of the total population, during the flowering of *Cornus* about 6 weeks later 24%, and for a two-week period at the end of the estival aspect, 25%. Homoptera built up from less than 1% of total population values in the *Prunus* period, to a value of 46% at the close of the estival, with a 10% value for the *Cornus* period. Such seasonal fluctuations in stratal structure do not obviate the concept of stratification. It becomes evident, however, that discernment of stratification of animals, if it does occur, is easier on the basis of short-time observations. Seasonal fluctuations, and even daily fluctuations tend to obscure the groupings. It is further suggested that the larger taxonomic groups (orders and families) may in many instances constitute a false premise on which to base recognition or evaluation of stratifiaction, at least in aerial strata. Innate life habits and the consequent habitat requirements within these groups are not sufficiently narrow to warrant such an attempt. The concept and analysis of stratification must be based primarily upon the vertical distribution of single species groups.

Considering first the daily patterns only for much of the estival aspect, it is seen that total populations in the herb stratum in true prairie subsere and postclimax tall-grass showed related but somewhat different diel curves. The night P.M. population produced the highest value in both of these stations; in the subseral prairie the night A.M. population was lowest, in the tall-grass the day A.M. population was lowest. On the basis of values gathered within shorter periods within the estival aspect, however, the daily curves for the two grassland stations more closely approach a common pattern (Figs. 31 and 33). This curve is at variance with the findings of Davidson and Shackleford (1929) who state that the herb population (in prairie in Oklahoma) "reached its daily maximum between midnight and three A.M., and had a second lesser peak between noon and three P.M." Differences in timing of collections in the two studies may in part account for these discrepancies

in fluctuation patterns. These authors concluded that larger numbers of specimens were taken in their collections due to inactivity of the insects during the warmest and coldest portion of the 24 hour cycle. It is suggested here that unless the warm part of the cycle suffered extremely high air temperatures during the period of their study (April and May), inactivity would not characterize that part of the day. The curves shown here do not bear out this conclusion, since in this study the fewest individuals were taken during the coldest of the four divisions of the 24 hour cycle, the greatest during a period of intermediate temperatures; during the period of high temperature intermediate numbers were collected.

During the field operations it seemed that because of heavy dews and the consequent saturation of the sweep net while making night collections, considerable portions of the populations of such soft and minute forms as leafhoppers might not be retrieved from the net if, indeed, they were swept from the vegetation. Examination of Table 32 and of Figure 36 shows, however, that, though some specimens may have been lost, the night collections were much of the time taking higher numbers than were the day sweeps. In this connection it is also of interest to point out that night sweep values for *Balclutha abdominalis* in the estival and autumnal aspects were, respectively, 69.8% and 69.5% those of the day sweep values, in the upland station, although the estival abundance was four times the autumnal.

It is noteworthy that during the estival period and again in the late autumnal, the day sweeps produced more individuals than the night sweeps in the grassland stations, while during the interim the night sweeps were in the ascendancy. This would suggest either (1) the seasonal and transitory presence of night feeders in the popualtion which spent the day low on the grasses or on the ground surface, or (2) different daily fluctuation patterns due to changing patterns of factor shifts before and after the warmest part of the year.

The physiological responses producing the apparent downward movement of the invertebrate populations in the shrub area are not clear. Because of cold air drainage, so evident in ravines on still summer nights, it seems that temperatures would be lowest at the ground surface. It has often been pointed out that animals do migrate from situations of apparently unfavorable environmental conditions to those which appear more favorable, and this, with "the presence of an 'innate rhythm' " is suggested by Carpenter (1935) as possible causes of population fluctuations. Downward movement at night of animals occupying the shrub stratum during the daytime, where high afternoon temperatures presumably obtain during the summer and evaporation rates approach those in open grassland (Fig. 13), must result from altered physiological needs resulting possibly in the absence of the light factor. It is not impossible that many of the shrub stratum forms do not migrate downward in the usual sense, but literally fall to the herb stratum. The answer to this problem will be found in closer scrutiny of key species in these populations and their physiological life histories.

A reciprocal upward nocturnal movement of ground surface forms was shown by the appearance of certain spiders, and especially the tenebrionid beetle, *Eleodes opaca,* all of which occurred abundantly in pitfall collections, in night sweeps in the herb stratum of all three stations.

There are obviously four major problems posed by these data: (1) Were

different numbers of invertebrates taken in the herb and shrub strata at different times of the daily cycle because of (a) fluctuations in animal numbers within those strata during that period, or (b) because different combinations of physical factors so affected collecting techniques and the response of the animals to those techniques that differentials in take indicate fluctuations that are more apparent than real; (2) if the animals were actually less numerous in one or the other of the strata during a given part of the 24 hours than at other periods studied, whence did they migrate; (3) what factor or combination of factors dictated their movements; and (4) what accounts for the differences in estival and autumnal diurnal patterns of total populations?

While the effects of changes in physical factors of the atmosphere upon invertebrate populations are probably most easily observed in vertical and recurrent daily fluctuations, responses of invertebrates to non-rhythmic shifts in aerial factors were also apparent. Population depressions occurred in all aerial strata coincidentally with the annual peak of temperature (in 1938) which was accompanied by a low in relative humidity values, a minor high in wind velocity, and a distinct peak of evaporation rates. As a matter of fact, this seeming extreme of environmental stress apparently "notched" total population peaks in these situations. Here, indeed, is suggested a period of inactivity produced in part by high temperatures, but it did not result in the capture of more insects—rather, fewer were taken indicating some movement out of the aerial (epiphytic) strata. This decline in invertebrate populations was especially marked in the more moist habitats, i.e., the tall grass and deciduous shrub, and might, as concluded by Davidson and Shackleford, indicate accelerated activity. Movement to more moist, cooler situations, probably downward, is most convincingly indicated, however.

Autumnal peaks of population tended to accompany or immediately follow a well defined secondary peak of temperature in September and October of 1938. The temperature depression of early April, 1938 was reflected in lowered epiphytic population values which had just begun building up.

On the basis of described aspection and horizontal and vertical distribution and fluctuation of invertebrate (mostly arthropod) populations, the significance of prevalent species, as determined in this study, should be discussed. It has been suggested that the population characteristics of prevalent species, which are more readily analyzed than those of total populations, *may* indicate (or at least illustrate) the conditions and processes of habitats, and possibly various phenomena of total populations. For practical purposes in field studies the rank of prevalence as defined here would probably need not be determined. In fact, weaknesses have appeared in the designation of prevalence as employed here. For example, a species may acquire prevalence in a season other than the one in which its highest values are shown.

It is emphasized that numbers as such cannot be categorically significant. Satisfying the requirements of statistical analysis may not necessarily reveal the complex relationships of habitat and organic needs and responses. It is conceivable that certain species of lesser abundance might more nearly indicate the environmental offerings of a given habitat and the general requirements of the habitat's total population than any numerically superior species. Apparently more significant in the determination of indicator values than mere numbers is the degree of confinement to a given society. It is, thereby, obvious that the physiological life history of a species must be known before

indicator values can be definitely assigned. The fact that a single species may force a total population peak cannot be considered conclusive as regards indicator values. Such specific highs may be eruptive and short-lived, and reflect but little regarding the nature of the habitat or the total population. Predatory species, such as spiders, may leave a destroyed or disturbed habitat and move into another.

Despite these weaknesses, there is evidence that prevalent species do present some indicator values. However, it is probable that no single prevalent (or any one species) can possess indicator values for all ecological phenomena in any given terrestrial habitat, i.e., one may indicate integrity of a society, another horizontal movement, dependence on more than one habitat, and innate changes in environmental needs, another fluctuations of physical or biotic factors or both through vertical movements, etc. The ecologist must know more about an individual species than its numbers, absolute or relative, to realize and reliably take advantage of its peculiar values as an indicator. In short, a blanket statement of indicator values is probably not possible.

Three of seven prevalents determined for the subseral true prairie (Station 1) were also prevalent in the tall grass (Station 2), which produced eight prevalents. Station 1 had one prevalent prevailing in three strata. The shrub habitat (Station 3) had one prevalent prevailing in two strata, and Station 2 had no prevalents prevailing in more than one stratum. These data, showing a tendency for closer confinement of postclimax species to their respective strata, may on the basis of distribution (stratification) indicate deeper strata and greater diversity in stratal factors in the deeper vegetation, i.e., the shallower the vegetational cover the more telescoped the strata as recognized on the basis of factor gradients, and, therefore, perhaps weaker definition of stratal societies. This suggests that in shallow strata the "spilling over" of animals might obscure stratal responses—that integrity of stratal societies is mechanically easier to maintain in deeper strata.

Just as plant communities, the members of which are adapted to each other and to their common surroundings, are more reliable indicators than individual plants (Weaver and Clements 1938:454), it may be found that animal communities are more reliable as indicators of conditions and processes than are individual species. Plant ecologists have shown, also, that "the dominant species are the most important indicators, since they receive the full impact of the habitat usually year after year" (Weaver and Clements 1938:454). The significance of *dominance* in terrestrial habitats is, of course, well understood; the significance of *prevalence* (i.e., numerical superiority by whatever term it has been designated) is much less if at all evident. The role of a species in a community is determined by more criteria than its numerical rank. The pitfall studies reported here have suggested the importance of *volume* of each species population in its biological significance within its community (Fig. 17). A prevalent species may produce much less bulk than a numerically inferior species. On the other hand, a minute species if present in great abundance might produce a greater volume than several less abundant, larger, and conspicuous species.

The naming of communities (societies, etc.) on the basis of numerical superiority of a few animal species (predominance of Shelford) supposes biological significance or indicator value. This predication needs examination. It is apparent that the various prevalents as determined in this study may indi-

cate different conditions and processes of habitat, but that they are not consistently or equally useful. Before the name of any animal in a terrestrial habitat can be assigned to its community with ecological honesty, the life history of that species, and especially its influence upon the habitat, termed *reaction,* must be known in detail. Its effects upon the other organisms of the community, called *coaction,* must likewise be known.

Prevalence, while it may serve as an indication of possession by the prevalent of significant biotic or diagnostic value, does not necessarily establish the role of the species in the economy of the community. "The importance of any organism in the household of nature is primarily a matter of food; on the one hand, the amount which the organism consumes, and on the other, the amount it supplies for other species. This, in turn, depends upon the abundance of the species and on its size and rate of metabolism" (Young 1938). Neither does prevalence, or by whatever term simple numerical superiority is designated, submit a valid criterion on which to base the naming of communities. It is suggested that the role of an animal species in the complex bio-ecological processes of reaction and coaction shall determine its qualification as a community constituent upon which to establish the name of the community. Such fundamental significance is not ascertained with the expediency afforded by the superficial counting of more or less individuals. The effect upon vegetation is of prime importance in the ecological evaluation of animal species and their place in the classification of terrestrial communities. The measurement of such effects by invertebrate species is faced with many difficulties.

This importance of relationship to vegetation, probably more specifically to the dominant species, suggests a possible significance in the consistent occurence of a species throughout a unit of vegetation whether climax or seral, and the concept of *paradominance.* For example, suppose that samples of invertebrate populations are made in large numbers of true prairie remnants showing climax structure, i.e., normal abundance of dominant grasses. The consistent presence of a certain species of insect is revealed. Comparable collections in prairie where drought or other disturbances have largely or entirely eliminated the dominants, show inconsistent occurrences or the complete absence of this species. The insect is indicated to be a concomitant of one or more of the dominant grasses, and could be assigned the role of *paradominant.* This would be an ecological designation based upon *frequency,* not upon abundance or influence. A species could, however, simultaneously be paradominant, prevalent, and influent. Weaver and Clements (1938) state that "the visible unity of the climax is due primarily to the dominants or controlling species." If the concept of paradominance is valid this statement might be reworded to say that "the visible unity of the climax is due primarily to the dominants and the paradominants, or the controlling plant species and their accompanying animal species."

These considerations of the volume and frequency values of a species population further suggest the possible ecological importance of those species presenting relatively low numerical values. Although the prairie studied was not in climax (due to recurrent drought) certain species which were either subprevalent or without designated rank may be exemplary. The walking stick, *Diapheromera veliei,* the chrysomelid beetles, *Pachybrachys luridus* and *P. litigiosus,* and the scarabeid, *Phyllophaga lanceolata,* because of their size or

frequency, did much to characterize the apparent structure of the invertebrate fauna of the prairie tract studied. Their known predilections for prairie plants suggest further important relationships. Yet, of these four consistently conspicuous and certainly characteristic species only one attained even subprevalence.

The marked decrease or disappearance of a so-called paradominant in response to losses suffered by the dominants is, of course, hypothetical. It is probable that such responses would show considerable lag, that disappearance, if ever effected, would be gradual. It is of some interest to note in this connection that the three species of beetles which attained prevalent values and two species which showed subprevalent values in this study are not listed as having been taken by Whelan (1936) in the same tract during 1928-30. Differences in collecting methods may have accounted for their absence in Whelan's list, however.

APPRAISAL OF METHODS

A comprehensive appraisal of the field methods used in this investigation is probably not possible on the basis of this short-time study, nor desirable in this report. Certain weaknesses were outstanding, however, and, though probably already recognized by many workers, should be briefly mentioned.

The problems involved in sampling the invertebrate populations of the soil and litter have been ably discussed at length by King (1939). It is felt that in this study the soil and litter samples were too few in number to yield conclusive data, probably due to (1) the unequal horizontal distribution of the invertebrates in these two strata, also pointed out by Dowdy (1944a), Blake (1945), and others, (2) inefficiency of the washing technique used for securing invertebrates from the one-third cubic foot soil sample, and (3) limitations of the investigator in sorting the animals from the debris of the litter samples.

While the sweep net continues to be the best device for sampling epiphytic and aerial populations of invertebrates, it is probable that sweep samples do not secure the whole picture (see also Muma and Muma 1949). The possible inadequacy of sweeps in sampling grasshopper populations and the complicating effects of dew have already been mentioned. The sweep net obviously does not sample any populations concentrated at or very near the bases of herbs, a distribution thought possibly to have occurred in this study under the telescoping effect of lowered temperatures on stratification, and left undetermined. The physical difficulties and the inefficiency of sampling the invertebrate population in such head-high shrubby vegetation as wild plums with a sweep net is immediately and painfully evident to the investigator. Only the periphery of such cover can be sampled; the interior of the shrubby thickets were often "alive" with aerial activity of flies, a stratal society that defied sampling with a sweep net because of the nature of the woody cover. Even in cover which is readily sampled with the net continuous care must be exercised to maintain a standard. Wind, darkness, terrain, variations in height of the vegetation, and fatigue of the investigator all serve to operate against securing the desired standardization of samples. It is probable that in most community studies carried on to date sweep samples, although made and handled with relative care, have left some of the story of populations undiscovered because of too infrequent use. Only high frequency and hard work can in part com-

pensate for the weaknesses inherent in the sweep net sampling technique.

While the alcohol pitfall method of collecting devised and used in this study is remarkably easy, it cannot be considered as a sampling method, at least not in the same sense as other methods. Its gather is continuous and dependent upon the movement of the individual animals. It may, thereby, be more efficient as a measure of activity than of population density, and as such may be most valuable in determining activity patterns in the ground surface populations of invertebrates thereby serving best as an adjunct to true sampling procedures. In this connection, Muma and Muma (1949) have pointed out the heavy preponderance of one sex or the other of certain prairie spiders in pitfall collections. The alcohol pitfall has the advantages of (1) operating in the absence of the investigator and thereby upon an undisturbed fauna, and (2) having its periods of take readily broken down into any subdivision of time that is desired. Its fixed position may result in thinning of the population in the immediate vicinity of gather, a possible weakness determinable by experimentation.

Finally, the following suggestions are offered toward possible improvements in studies designed merely or primarily for ascertaining population and community phenomena:

1. Thorough study can best be accomplished on one habitat at a time. Simultaneous comparative studies are fascinating and for many purposes desirable or indispensable, but the mimimal standards of sampling and the weight of data gathered can be beyond the limitations of the investigator.

2. A habitat that is distinctly uniform over a large area will yield the most reliable community information. Dowdy (1944a:220) has pointed out that "uniformity of habitat makes for a limited number of species but the number of specimens might be great." These conditions lend strongly to ease of operations as well as reliability of data gathered.

3. To base community (society) nomenclature upon short-time studies appears ill-advised (see also Blake 1931). The naming of ephemeral and possibly non-recurrent though striking groupings of invertebrates results only in "cluttering the literature." Any investigation carried on for less than three years, albeit continuously, must be considered "short-time."

4. In studies on stratification and daily fluctuations mean values may be misleading. Detailed, on-the-spot, simultaneous (in so far as possible) measurements of both populations and physical factors are probably more reliable.

5. Detailed life history studies on as many species as possible within the habitat will help complete the picture of habitat-fauna relationships. These key species may be initially indicated by any combination of three criteria—prevalence, paradominance, or endemicity.

6. Laboratory studies may be necessary in analyzing and evaluating the responses of key species to environmental shifts as measured in the field.

7. The need for perfecting and employing methods of sampling the invertebrate populations of more and shallower aerial or epiphytic strata within the many kinds of cover is evident; for example, this study could have profited from unadulterated samples of the animals present on the herbs from 0-6 inches above the surface of the ground, or even within 0-2 inches.

Summary

The invertebrate fauna and environmental factors of upland true prairie (subseral in response to recurrent drought) and associated units of postclimax tall grass and postclimax deciduous shrub were quantitatively studied from November 2, 1937, to November 4, 1939.

Attention was focused upon (a) the differences in the environmental complexes within the three habitats studied, (b) the faunal interrelationships of these three stations, (c) horizontal and vertical movements as exhibited by stratal, seasonal, and diel values of total populations as sampled, and (d) the strato-seasonal activities of prevalent species.

Prevalent species were determined on the basis of strato-seasonal abundance, i.e., that species which showed the highest seasonal population within a given stratum thereby attained the rank of prevalent for that season, a designation which indicates only that the species prevailed numerically in that stratum.

A species which exhibited a seasonal population less than that of the prevalent, and which may or may not have equalled the frequency values of the prevalent, but which exceeded the population values of the latter at one or more brief intervals, even in any one sample collection, was considered as possessing subprevalent rank.

Four strata were studied in the true prairie subsere and postclimax tall grass, namely (a) soil, (b) litter, (c) ground surface, and (d) herb, with the addition of (e) the shrub stratum in the postclimax deciduous shrub station. The soil stratum was sampled to a depth of 10 cm. (4 inches), always beneath the one square foot of litter collected for examination from the litter stratum. The ground surface invertebrate fauna was studied by use of an alcohol pitfall, an apparatus which does not measure any given unit of population at any given time, but which does appear to indicate population trends. The population of the herb and shrub strata were sampled by the sweep net method at 0-75 cm. above the ground surface in the herb and at the 1-2 meter level in the shrub.

Seasonal studies (sweeps, and litter and soil sampling) were carried on from November 2, 1937 to March 20, 1939, the day-night (diurnation) studies (sweeps only) from June 12 to October 21, 1938, and the pitfall (ground surface) studies from April 8 to November 4, 1939. This study is based upon the collection and examination of 81,811 specimens of invertebrates.

The term invertebrate as herein employed includes only the phyla Annelida and Mollusca and the classes Arachnida (excepting the Order Acarina) and Insects (excepting the orders Collembola, Thysanoptera, and Corrodentia).

This study was conducted within a continuous tract of native true prairie one-half section in extent (Township 10 N.—Range 5 E., Section 2, east half), which is located five and one-half miles west and three miles north of Lincoln, Nebraska. Haying operations have constituted the only cultural disturbance to which the vegetation has been subjected, with the exception of grazing by a small band of horses during one winter about 1933.

Severe drought had been in progress for about four years in the true prairie region when this investigation was initiated. The grassland studied was in a generally reverse though fluctuating succession from true prairie to mixed prairie—a subsere induced by drought and marked by great, rapid, and com-

plex changes in the vegetation. Postclimaxes were less affected by the drought.

The true prairie subsere station was placed slightly below the rounded top of the next to the highest hill of the tract, on a south-southeast slope. *Stipa spartea, Bouteloua curtipendula, Andropogon scoparius, Koeleria cristata,* and *Sporobolus heterolepis* were the most abundant grasses, much bare soil surface being evident with little or no litter. *Psoralea floribunda* was the most prominent forb. *Erigeron ramosus* was markedly abundant in the subseral true prairie substations.

Average conditions of postclimax tall-grass habitat were found in a ravine which was centrally located in the tract and which drained to the south-southwest. Station 2 was established here, where *Andropogon furcatus, Elymus canadensis, Panicum virgatum,* and *Poa pratensis* characterized the vegetation, forming a dense sod, with *Aster* the prominent forb.

Station 3 was located near the northeast corner of the tract. Here an area some 20 yards long and about 15 yards wide was rather densely covered by *Cornus stolonifera, Prunus americana, Rhus glabra,* and *Symphoricarpos occidentalis,* and presented an ecological "island."

Measurable environmental (micro-climatic) differences were found to exist in the three vegetational complexes, most conclusively shown for the aerial forces of wind and evaporation stress and for the soil moisture factor. The horizontal gradient of wind velocity was steepest between the subseral true prairie and the postclimax tall-grass stations, while the gradients of relative humidity, evaporation rate, and soil moisture showed their highest values in the shrub station, indicating an approach here to the environmental conditions of forest margin.

The invertebrate communities of these three habitats exhibited recognizable distinctness, the structure of those of the tall grass and subseral true prairie being much more closely related than that of either of these to the communities of the deciduous shrub habitat.

Faunistic expression of the prevernal aspect preceded floristic expression.

Seasonal societies of invertebrates showed well defined correlations with floristic aspects, affording an indication of biotic influences in chronological distribution as expressed in innate rhythms of life histories. The integrity of seasonal societies, as determined by analysis of prevalent and subprevalent species was evident, though not infallible.

A few species occupied important rank in all three vegetational complexes, showing that inherent activity patterns and physiological needs of key species must be known before evaluation of populations can be determined and the biotic valence of their component parts be established.

Key species may be indicated by prevalence. Endemicity and paradominance, the latter a concept of ecological significance based on frequency of occurrence, may also define key species.

Prevalence, attained in a given season or stratum, does not necessarily denote that the greatest yearly abundance of the species is reached in that society, i.e., fluctuations in composition of communities, either spatial or chronological, may bring into prevalence a species which has not significantly altered its absolute population value.

Extremes of high temperature, wind velocity, and evaporation seemed to have less effect upon the invertebrate population of the true prairie subsere than upon those of the postclimax habitats.

Horizontal movements of insects from one community to another were evident, especially by members of the order Hemiptera during the prevernal and late autumnal aspects. These may be interpreted as resulting from changes in food and cover requirements. Responses to food source produce a horizontal distribution characteristic of periods of heightened physiological rate, while responses to cover requirements result in a horizontal-vertical redistribution which characterizes periods of lowered physiological rate.

Stratification of physical factors was discernible even in the comparatively shallow herbaceous cover of the prairie.

Vertical movements, in part characterizing the daily pattern of invertebrate population activities, apparently occurred in response to daily shifts in physical factors, especially in the deeper cover of the shrub station. The relative importance of causative factors in this relationship is not clear.

Populations of invertebrates in the grassland stations displayed two high points—one in the estival aspect, another in the latter half of the autumnal aspect.

The herb population of the deciduous shrub, proportionately higher than that of the grassland, exhibited an enormous peak of abundance in late autumn. This appeared to be due largely to the emergence and increase of endemic and distinctly woodland or forest margin species at this time.

The shrub stratum showed its peak of invertebrate abundance in the prevernal-vernal period coincident with anthesis of *Prunus*.

Litter and soil populations reached their maxima in the hiemal aspect, while the invertebrates of the ground surface showed a pattern of population values similar to that of the herb stratum.

Invertebrate population peaks in all situations were for the most part due to the presence of one or a few species whose numbers build up, rather than to general and concurrent increases of the many species comprising the entire population.

Homoptera, Coleoptera, Orthoptera, Diptera, and Hymenoptera (Formicidae) generally characterized the invertebrate fauna of the upland true prairie (subseral) tract and its included postclimax areas during the period of the study. *Balclutha abdominalis* (Homoptera), *Oscinella coxendix* (Diptera), *Pachybrachys litigiosus* (Coleoptera), *Crematogaster lineolata* (Formicidae), and *Melanoplus bivittatus* (Orthoptera) constituted the most abundant species within each of these orders.

Balclutha abdominalis was the most important species taken on the basis of numbers, frequency, and distribution.

The subseral true prairie presented an invertebrate population (principally arthropods) which may be characterized as follows:

(a) The herb stratum population was comprised largely of Homoptera, Coleoptera, Orthoptera, Diptera, Formicidae, Araneida, winged Hymenoptera, and Hemiptera in that order of group abundance; that of the ground surface largely of Formicidae, Coleoptera, and Araneida in that order of group abundance; that of the litter stratum largely of Coleoptera, Formicidae, Araneida, and Annelida in that order of group abundance; and that of the soil stratum largely of Coleoptera and Annelida in that order of abundance.

(b) In the herb stratum the cicadellid leafhopper, *Balclutha abdominalis*, was the prevernal-vernal, estival, and autumnal prevalent, the fulgorid, *Delphacodes*, was the estival prevalent; in the soil surface stratum the carabid beetle,

Amara sp., was the prevernal-vernal prevalent, the ant, *Dorymyrmex pyramicus,* was the estival prevalent, the ant, *Crematogaster lineolata,* was the autumnal and early hiemal prevalent; in the litter stratum the enchytraeid earthworm, *Fridericia* spp., was the prevernal-vernal and estival prevalent, *Amara* sp. the autumnal prevalent, and *Piesma cinerea,* a bug. the hiemal prevalent. *Amara* was the annual prevalent in the soil stratum.

(c) Subprevalent or conspicuous in the estival aspect was the psyllid, *Aphalara veazei,* the walking stick, *Diapheromera veliei,* the May beetle, *Phyllophaga lanceolata,* and the chrysomellids, *Pachybrachys litigosus* and *P. luridus* in the herbs, the tenebrionid, *Eleodes opaca;* and the blister beetle, *Macrobasis segmentata* (Say) on the ground surface; in the autumnal aspect the fly, *Oscinella minor,* and the gryllid, *Oecanthus niveus,* helped characterize the herb society.

(d) Both herb and ground surface populations showed a major peak of abundance in the estival aspect and a less well defined autumnal high.

(e) Daily fluctuations in total numbers of invertebrates and in relative numbers of prevalent, subprevalent, and conspicuous species were found coincident with daily shifts in physical factors of the atmosphere in the herb stratum.

(f) Certain species found here in the estival and early autumnal aspects appeared largely dependent upon the postclimax habitats for hibernating cover.

(g) The true prairie (subseral) invertebrate communities were found to be structurally related to those of both postclimax habitats, most closely to those of the tall grass.

Analysis of the population patterns of prevalent species has illustrated the following ecological conditions or processes:

(a) Aspectional sequence of ravine and upland sites (postclimax and subseral vegetation): Prevernal precedence of the protected ravine sites (*Delphacodes* sp., *Piesma cinerea, Melanoplus bivittatus*); autumnal lag of the protected sites (*Crematogaster lineolata, Melanoplus bivittatus*).

(b) Pre-hibernation (autumnal) and post-hibernation (prevernal) movement, both horizontal and vertical, of a major crop pest (*Blissus leucopterus*) and other grassland species into tali-grass and shrub hibernation areas (*Balcluta abdominalis, Piesma cinerea, Lygus pratensis*).

(c) Wide distribution through several habitats at any given time, but with evident habitat preference (*Amara* sp., *Piesma cinerea, Balclutha abdominalis, Prenolepis imparis, Crematogaster lineolata, Melanoplus bivittatus*).

(d) Confinement to habitat (*Dorymyrmex pyramicus, Chalcoides fulvicornis, Geotomus robustus, Ataenius cognatus*).

(e) Stratal confinement (*Erythroneura* sp., *Dikraneura abnormis*).

(f) Deep stratal distribution, i.e., disregard for stratal barriers apparently regulatory upon other species (*Prenolepis imparis*).

(g) Operation of biological forces in the stratification of invertebrates: Coaction (*Prenolepis imparis, Anoecia graminis, Chalcoides fulvicornis*).

(h) Daily fluctuations (*Erythroneura* sp.).

(i) Seasonal integrity (*Amara* sp., *Dikraneura abnormis, Chalcoides fulvicornis*).

(j) Forcing of peaks of total population by singe species (*Geotomus robustus, Leiobunum* sp.).

REFERENCES

ADAMS, C. C. 1915—An ecological study of prairie and forest invertebrates. Bull. Ill. St. Lab. Nat. Hist. 11:28-280.

ADAMS, ROY HENRY 1941—Stratification, diurnal and seasonal migration of the animals in a deciduous forest. Ecol. Monog. 11:189-227.

AIKMAN, J. 1929—Distribution and structure of the forests of eastern Nebraska. Univ. Nebr. Studies 26:1-75.

ALBERTSON, F. W. AND J. E. WEAVER 1945—Injury and death or recovery of trees in prairie climate. Ecol. Monog. 15:393-433.

ALLRED, B. W. 1941—The significance of grassland ecology to the northern great plains. Discussion presented before the Northern Great Plains Grassland Conference, Mandan, South Dakota, June 26, 1941 (mimeographed).

BARE, ORLANDO S. (in manuscript)—A taxonomic study of Nebraska ants. Dept. of Entom. Univ. of Nebr.

BEALL, G. 1935—Study of arthropod populations by the method of sweeping. Ecology 16:216-225.

BEED, W. E. 1936—A preliminary study of the animal ecology of Nebraska short-grass plains grazed only by native mammals. Univ. of Nebr. Conserv. and Surv. Div. Bull. 10:1-33.

BLAKE, I. H. 1926—A comparison of the animal communities of coniferous and deciduous forests. Ill. Biol. Monog. 10:1-148.

———1931—Further studies on deciduous forest animal communities. Ecology 12:508-527.

———1945—An ecological reconnoissance in the Medicine Bow Mountains. Ecol. Monog. 15:207-242.

BRUNER, LAWRENCE 1900—A preliminary report of the insects affecting native grasses on our prairies and in meadows. Report of the Entomologist, Nebr. State Board of Agric. pp. 103-141.

CARPENTER, J. R. 1935—Fluctuations in biotic communities. I. Prairie-forest ecotone of central Illinois. Ecology 16:203-212.

———1936—Daily fluctuations in insect populations on the prairie-forest ecotone of North America. Comptes Rendus du XIIe Congres International de Zoologie—Lisbonne 1935:969-979.

———1937—Fluctuations in biotic communities. III. Aspection in a ravine sere in central Oklahoma. Ecology 18:80-92.

———1938—An ecological glossary. viii+306 pp. University of Oklahoma Press.

———1939a—The biome. Amer. Midl. Nat. 21:75-91.

———1939b—Fluctuations in biotic communities. V. Aspection in a mixed-grass prairie in central Oklahoma. Ibid. 22:420-435.

CHAPMAN, ROYAL N. 1939—Insect population problems in relation to insect outbreak. Ecol. Monog. 9:261-269.

CLEMENTS, F. E., J. E. WEAVER AND H. C. HANSON 1929—Plant competition. Carnegie Inst. Wash. Pub. 398. xvi+340 pp.

——— AND V. E. SHELFORD 1939—Bioecology. vi+425 pp. J. Wiley and Sons, Inc.

COMSTOCK, JOHN HENRY 1940—An introduction to entomology. 9th ed., revised. xix+1072 pp. Comstock Publishing Company.

DAVIDSON (SMITH) V. G. 1930—The tree layer society of maple-red oak climax forest. Ecology 11:601-606.

——— AND M. W. SHACKLEFORD 1929—Diurnal variations in the vernal invertebrate populations of a central Oklahoma prairie. Proc. Okla. Acad. Sci. 9:54-59.

DOWDY, W. W. 1944a—A community study of a disturbed deciduous forest area near Cleveland, Ohio, with special reference to invertebrates. Ecol. Monog. 14:193-222.

———1944b—The influence of temperature on vertical migration of invertebrates inhabiting different soil types. Ecology 25:449-460.

———1947—An ecological study of the Arthropoda of an oak-hickory forest with reference to stratification. Ibid. 28:418-439.

FERNALD, H. T. AND HAROLD T. SHEPARD 1942—Applied entomology. 4th ed. ix+400 pp. McGraw-Hill.

FICHTER, EDSON 1939—An ecological study of Wyoming spruce-fir forest arthropods with special reference to stratification. Ecol. Monog. 9:183-215.

———1941—Apparatus for the comparison of soil surface arthropod populations. Ecology 22:338-339.

GRAHAM, EDWARD H. 1941—Grasses in the conservation of soil and wildlife. U.S.D.A. (Prepared for use in the Soil Conservation Service, mimeographed.)
HERRICK, GLENN W. 1925—Manual of injurious insects. xxi+489 pp. Henry Holt.
HOOVER, M. M. 1939—Native and adapted grasses for conservation of soil and moisture in the Great Plains and western states. U.S.D.A. Farmers' Bull. 1812.
———, JAMES E. SMITH, JR., A. E. FERBER AND D. R. CORNELIUS 1947—Seed for regrassing Great Plains areas. Ibid. 1985.
KING, KENNETH M. 1927—A quantitative investigation of the fauna of native and ruderal associations at Saskatoon, Saskatchewan, with special reference to climatic influence. Abstract in Bull. Ecological Soc. Amer. 8(4):5.
———1939—Population studies of soil insects. Ecol. Monog. 9:270-286.
LEOPOLD, ALDO AND SARA ELIZABETH JONES 1947—A phenological record for Sauk and Dane Counties, Wisconsin, 1935-1945. Ibid. 17:81-122.
LOVELAND, G. A. 1920—Summary of the climatological data for the United States, Section 37—Southern Nebraska. U.S. Dept. Agr. Weather Bureau, pp. 1-2.
MCCLURE H. ELLIOTT 1938—Insect aerial populations. Ann. Ent. Soc. Amer. 31:504-513.
MUMA, MARTIN H, AND KATHERINE E. 1949—Studies on a population of prairie spiders. Ecology 30:485-503.
OSBORN, H. 1917—Control of meadow and pasture insects. Ohio Agr. Exp. Sta. Monthly Bull. 20:268-273.
———1939—Meadow and pasture insects. viii+288 pp. Educators' Press, Columbus, Ohio.
PARK, T. 1939—Analytical population studies in relation to general ecology. Amer. Midl. Nat. 21:235-253.
PATCH, EDITH M. 1938—Food-plant catalogue of the aphids of the world. Maine Agr. Exp. Station Bull. 393.
PEAIRS, LEONARD M. 1941—Insect pests of farm, garden, and orchard. xvii+549 pp. John Wiley and Sons.
PEARSE, A. S. 1946—Observations on the microfauna of the Duke Forest. Ecol. Monog. 16:127-150.
ROBERTSON, J. H. 1939—A quantitative study of true prairie vegetation after three years of extreme drought. Ibid. 9:431-492.
SHACKLEFORD, M. W. 1929—Animal communities of an Illinois prairie. Ecology 10:126-154.
———1931—Autumnal herb societies of an Oklahoma prairie in 1927, 1928, and 1930. Okla. Acad. Sci. Proc. 11:13-14.
———1935—Seasonal variations in the invertebrate population of a central Oklahoma prairie, November, 1933 to November, 1934. Ibid. 15:69-72.
——— AND M. J. BROWN 1929—A comparison of the autumnal society of prairie invertebrates and of coincident weather conditions of 1927 and 1928. Ibid. 9:20-23.
——— AND V. G. SMITH 1928—Autumnal animal communities of a prairie. Ibid. 8:80-83.
SHELFORD, V. E. 1911—Physiological animal geography. Journ. Morph. 22:537-618.
———1926—Terms and concepts in animal ecology. (Note) Ecology 7:389.
———1929—Laboratory and field ecology. xii+608 pp. Williams and Wilkins.
———1930—Ways and means of improving the quality of investigation and publication in animal ecology. Ecology 11:235-236.
———1932—Basic principles of the classification of communities and habitats and the use of terms. Ibid. 13:105-120.
——— AND S. OLSON 1935—Sere, climax and influent animals with special reference to the transcontinental coniferous forest of N. A. Ibid. 16:375-402.
SMITH, HARRY S. 1939—Insect populations in relation to biological control. Ecol. Monog. 9:311-320.
STEIGER, T. L. 1930—Structure of prairie vegetation. Ecology 11:170-217.
SWENK, MYRON H. AND H. DOUGLAS TATE 1941—Control of the chinch bug in Nebraska. Univ. of Nebr. Coll. of Agric. Exp. Station Circular 61.
TOWNSEND, CHAS. H. T. 1924—An analysis of insect environments and response. Ecology 5:14-25.
U. S. D. A. 1948 Grass: Yearbook of Agriculture. xiv+892 pp. U. S. Dept. of Agric.
VESTAL, A. G. 1914—Internal relations of terrestrial associations. Am. Nat. 48:413-445.

WEAVER, J. E. 1943—Replacement of true prairie by mixed prairie in eastern Nebraska and Kansas. Ecology 24:421-434.
——— AND F. W. ALBERTSON 1944—Nature and degree of recovery of grassland from the great drought of 1933 to 1940. Ecol. Monog. 14:393-479.
——— AND F. E. CLEMENTS 1938—Plant ecology. xxii+601 pp. Mc-Graw-Hill.
——— AND T. J. FITZPATRICK 1934—The prairie. Ecol. Monog. 4:109-295.
——— AND W. J. HIMMEL 1931—The environment of the prairie. Univ. of Nebr. Cons. and Surv. Bull. 5.
WEESE, A. O. 1924—Animal ecology of an Illinois elm-maple forest. Ill. Biol. Monog. 1:1-93.
WHELAN, DON B. 1927—The winter fauna of the bunch-grasses in eastern Kansas. Ecology 8:94-97.
———1936a—Coleoptera of an original prairie area in eastern Nebraska. Journ. Kans. Ent. Soc. 9:111-115.
———1936b—Some mammals of an eastern Nebraska prairie. Trans. Kansas Acad. of Sci. 39:365-366.
———1938—Orthoptera of an eastern Nebraska prairie. Journ. Kans. Ent. Soc. 11:3-6.
———1940—Birds of a surviving area of original prairie land in eastern Nebraska. Nebraska Bird Review 8:50-55.
YOUNG, A. D. 1938—The life at Flathead Lake, Montana. Ecol. Monog. 5:91-163.

TABLE 1.—Amount of rainfall* recorded by rain gauge in Station 1 (true prairie subsere).

Two-week period ending	Inches	Total for season		Two-week period ending	Inches	Total for season	
1938							
Jan. 18	0.01			Dec. 17	0.00		
Jan. 31	0.26			Dec. 31	0.16*		
Feb. 14	0.00			1939			
Feb. 28	1.44†			Jan. 14	0.15		
Mar. 14	0.55			Jan. 28	0.22		
Mar. 28	1.57	3.88	Hiemal	Feb. 11	0.00		
Apr. 11	1.04†			Feb. 25	2.28*		
Apr. 25	2.44			Mar. 11	1.32		
May 9	3.99			Mar. 25	1.08	6.90	Hiemal
May 23	1.17	8.64	Prevernal-vernal	Apr. 8	1.68		
				Apr. 22	0.91		
				May 6	0.06		
Jun. 6	0.93			May 20	0.25	2.90	Prevernal-vernal
Jun. 20	2.38						
Jul. 4	4.65			Jun. 3	1.92		
Jul. 18	0.33			Jun. 17	1.67		
Aug. 1	0.42	8.71	Estival	Jul. 1	2.57		
Aug. 15	1.14			Jul. 15	1.60		
Aug. 29	0.52			Jul. 29	1.06	8.82	Estival
Sep. 12	4.92			Aug. 12	1.84		
Sep. 24	0.82			Aug. 26	0.50		
Oct. 8	0.00			Sep. 9	0.00		
Oct. 22	0.72	8.12	Autumnal	Sep. 23	0.10		
Nov. 5	1.66			Oct. 7	0.69		
Nov. 19	0.03			Oct. 21	0.28	3.41	Autumnal
Dec. 3	0.00			Nov. 4	0.00		

* Some winter records determined from melted snow probably not exact.
† Melted snow.

TABLE 2.—Air temperature in degrees F. at 0.1 meter above the surface of the ground in Station 1 (true prairie subsere).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1937							
Nov. 16	76.0	21.5	60.6	36.6	46.9	54.5	23.9
Nov. 30	60.5	0.0	36.2	18.8	26.2	60.5	17.3
Dec. 14	53.0	0.0	32.2	15.3	22.7	53.0	16.8
Dec. 21*	48.0	20.5	39.7	23.4	30.3	27.5	16.3
1938							
Jan. 4	62.5	12.5	46.0	23.1	32.8	50.0	22.8
Jan. 18	56.5	0.0	42.8	20.0	28.4	56.5	22.8
Jan. 31*	62.0	—7.5	33.8	16.4	25.1	69.5	17.4
Feb. 14	67.0	9.5	44.3	24.0	33.3	57.5	20.3
Feb. 28†	46.0	8.5	33.3	22.8	27.2	37.5	11.2
Mar. 14	74.0	20.0	48.7	31.2	38.4	54.0	17.6
Mar. 28	81.5	32.5	59.2	39.7	49.2	49.0	19.5
Apr. 11	68.0	21.5	50.0	33.1	39.5	46.5	16.9
Apr. 25	83.0	34.0	70.5	48.8	59.0	49.0	21.7
May 9	82.0	33.5	71.0	51.2	58.3	48.5	19.8
May 23	77.0	41.0	65.5	50.1	58.3	36.0	15.3
Jun. 6	84.5	42.5	76.1	56.0	65.5	42.0	20.2
Jun. 20	84.5	50.0	80.2	59.1	69.2	34.5	21.1
Jul. 4	101.0	53.0	87.0	65.6	74.8	48.0	21.4
Jul. 18†	102.0	59.0	91.0	66.0	78.4	43.0	25.0
Aug. 1	103.0	58.5	97.3	65.0	79.4	44.5	32.2
Aug. 15	112.0	58.5	99.3	71.1	83.7	53.5	27.9
Aug. 29	107.5	56.0	92.0	66.7	78.5	51.5	25.3
Sep. 12	103.0	61.0	91.6	57.6	77.6	42.0	24.0
Sep. 24*	100.0	38.0	80.0	52.0	63.8	62.0	28.0
Oct. 8	98.5	52.0	92.5	58.0	73.4	46.5	34.6
Oct. 22	92.0	37.0	81.0	51.7	64.6	55.0	29.3
Nov. 5	87.0	32.5	73.2	43.7	53.7	54.5	29.4
Nov. 19	64.0	19.0	51.6	30.2	40.2	45.0	21.4
Dec. 3	68.0	2.0	43.8	18.0	30.3	66.0	25.8
Dec. 17	57.0	6.0	43.4	21.3	30.6	51.0	22.1
Dec. 31	—	—	—	—	—	—	—
1939							
Jan. 14	67.5	15.0	48.4	24.0	33.3	52.5	24.5
Jan. 28	58.0	2.5	37.0	17.2	25.7	45.5	19.8
Feb. 11‡	54.0	—5.0	42.8	17.7	25.9	59.0	25.1
Feb. 25	47.0	—6.0	29.3	11.0	19.5	53.0	18.3
Mar. 11	52.0	11.0	37.0	22.6	28.7	41.0	14.3
Mar. 25	83.0	12.5	57.3	29.0	41.6	70.5	28.4
Apr. 8	76.0	23.5	52.0	32.7	41.3	52.5	19.2
Apr. 22	73.5	17.0	58.1	36.3	44.7	56.5	21.6
May 6	88.0	42.0	81.0	51.6	65.5	46.0	29.4
May 20	95.0	40.0	79.6	50.7	64.2	55.0	29.0
Jun. 3	100.0	48.0	87.8	59.8	72.7	52.0	28.0
Jun. 17†	101.0	52.5	79.5	61.0	70.0	48.5	18.5
Jul. 1	100.0	56.5	91.0	63.0	75.1	43.5	28.1
Jul. 15	113.0	61.5	96.4	69.0	82.2	41.5	27.4
Jul. 29	110.5	61.0	97.3	67.1	80.9	49.5	30.1
Aug. 12	104.0	52.0	91.4	62.7	75.9	52.0	28.7
Aug. 26	98.0	49.0	88.7	60.2	72.8	49.0	28.5
Sep. 9	108.0	58.0	98.0	66.9	81.0	50.0	31.1
Sep. 23	104.0	47.5	95.1	60.7	77.3	56.5	34.4
Oct. 7	100.5	30.5	80.8	44.0	60.1	70.0	37.0
Oct. 21	84.0	26.5	70.1	40.8	54.1	57.5	29.3
Nov. 4	84.0	16.5	62.4	33.7	46.9	67.5	28.7

* Short period. † Record for 1 week. ‡ Record for 12 days.

TABLE 3.—Air temperature in degrees F. at 0.1 meter above the surface of the ground in Station 2 (postclimax tall grass).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Jan. 18	63.0	—10.5	49.9	10.6	25.7	73.5	39.2
Jan. 31*	66.0	—22.0	36.3	12.0	24.1	88.0	24.3
Feb. 14	69.5	5.5	48.3	20.2	32.5	64.0	28.1
Feb. 28	52.0	—5.0	30.7	13.2	21.5	57.0	16.8
Mar. 14	81.0	13.0	52.3	27.8	40.5	68.0	25.2
Mar. 28†	87.0	26.0	65.8	34.8	48.2	61.0	31.0
Apr. 11	71.5	13.5	53.0	28.7	38.5	58.0	24.3
Apr. 25	85.0	25.5	74.3	45.4	58.0	59.5	28.9
May 9	86.0	29.5	68.9	44.8	57.8	56.5	24.1
May 23	80.5	36.5	69.6	46.2	57.3	44.0	23.4
Jun. 6	88.0	35.5	79.4	51.8	64.9	52.5	27.6
Jun. 20	89.0	45.5	89.7	56.5	68.3	43.5	34.1
Jul. 4	101.5	51.5	86.8	64.6	74.1	50.0	22.2
Jul. 18‡	101.0	52.0	91.5	61.5	76.1	49.0	30.0
Aug. 1	103.5	51.5	96.0	59.9	76.4	52.0	36.1
Aug. 15	107.5	46.5	99.6	68.2	82.5	61.0	31.4
Aug. 29	107.0	47.0	91.0	62.8	76.0	60.0	28.1
Sep. 12	101.0	57.0	91.5	64.4	76.3	44.0	27.0
Sep. 24*	99.5	30.0	80.3	45.9	60.6	69.5	34.3
Oct. 8	98.0	43.5	89.9	51.3	68.2	54.5	38.6
Oct. 22	92.0	28.0	80.8	45.4	60.6	64.0	35.4
Nov. 5	85.5	23.0	71.7	37.9	50.2	65.5	33.7
Nov. 19	69.0	12.5	55.3	22.2	37.9	65.5	31.5
Dec. 3	74.5	—2.0	47.9	16.0	28.5	76.5	31.8
Dec. 17	61.0	2.0	47.5	18.9	32.2	59.0	28.5
Dec. 31	55.0	—2.0	39.4	11.5	24.4	57.0	27.9
1939							
Jan. 14	74.0	11.5	55.1	22.9	34.7	62.5	32.1
Jan. 28	67.0	4.5	39.3	12.5	25.7	71.5	25.3
Feb. 11	60.0	14.0	59.1	34.3	23.1	66.0	24.8
Feb. 25	49.0	—10.0	32.0	6.4	19.0	59.0	25.6
Mar. 11	49.5	8.5	37.0	20.6	27.6	41.0	16.4
Mar. 25	87.0	11.5	60.0	27.7	41.8	75.5	32.4
Apr. 8	67.0	17.0	51.5	29.6	39.4	50.0	21.9
Apr. 22	74.0	9.0	58.8	33.4	44.4	65.0	26.0
May 6‡	89.0	37.0	82.3	45.8	63.1	52.0	34.9
May 20	96.0	31.5	79.1	44.8	62.3	64.5	34.3
Jun. 3	102.5	42.5	88.7	56.4	71.9	60.0	32.4
Jun. 17	103.0	50.0	85.3	56.9	70.1	53.0	30.7
Jul. 1	99.0	49.0	91.1	58.5	74.1	50.0	32.5
Jul. 15	106.5	55.0	96.5	64.5	79.9	51.1	32.0
Jul. 29	108.5	53.0	96.6	62.4	79.0	55.5	34.2
Aug. 12	108.5	45.5	95.0	51.4	75.1	63.0	36.4
Aug. 26‡	104.5	41.5	90.1	55.9	71.8	63.0	34.2
Sep. 9‡	107.5	49.0	98.8	62.2	81.0	58.5	36.6
Sep. 23	105.0	38.5	98.2	57.0	76.7	66.5	41.1
Oct. 7	107.0	22.0	80.3	44.0	60.0	85.0	36.3
Oct. 21	85.0	17.0	70.8	33.6	50.8	68.0	37.2
Nov. 4‡	89.5	14.0	64.9	28.9	44.8	75.5	35.2

* Short period. † Record for 1 week. ‡ Record for 12 days.

TABLE 4.—Air temperature in degrees F. at 0.1 meter above the surface of the ground in Station 3 (postclimax deciduous shrub).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Jan. 18	55.0	—10.0	42.6	14.1	25.3	65.0	28.4
Jan. 31*	59.0	—19.5	34.5	15.9	24.4	78.5	19.4
Feb. 14	67.0	4.0	46.0	22.0	32.5	63.0	24.0
Feb. 28	47.0	—2.0	27.8	14.6	20.8	49.0	13.2
Mar. 14	73.0	15.0	48.4	27.6	30.6	58.0	20.8
Mar. 28	82.0	21.5	65.4	32.3	45.8	60.5	33.0
Apr. 11	73.0	14.5	52.0	30.2	39.9	58.5	21.8
Apr. 25	86.0	24.5	75.2	45.7	58.1	61.5	29.3
May 9	90.0	32.0	74.9	48.7	59.7	58.0	26.2
May 23	84.0	36.0	71.0	48.5	58.7	48.0	22.5
Jun. 6	90.0	36.0	80.8	52.9	65.1	54.0	27.9
Jun. 20	90.0	49.0	84.1	58.5	68.1	41.0	25.6
Jul. 4	101.0	50.0	89.6	66.4	75.0	51.0	23.1
Jul. 18	100.0	53.0	92.7	64.6	76.8	47.0	28.0
Aug. 1	96.0	51.0	89.7	59.6	72.1	45.0	30.1
Aug. 15	103.5	49.5	94.9	66.7	79.2	54.0	28.1
Aug. 29	101.5	49.5	87.8	62.6	73.5	52.0	25.1
Sep. 12	93.5	57.0	86.5	64.4	73.0	36.5	22.0
Sep. 24*	83.0	32.0	73.5	45.8	50.4	51.0	27.7
Oct. 8	86.0	43.5	80.9	49.1	62.6	42.5	31.9
Oct. 22	81.0	30.5	73.5	44.7	56.5	50.5	28.8
Nov. 5	77.0	26.0	64.6	36.2	48.0	51.0	28.4
Nov. 19	63.5	15.5	52.4	26.4	37.3	48.0	26.0
Dec. 3	64.0	—1.5	44.4	13.4	26.8	65.5	29.3
Dec. 17	58.0	2.0	44.5	18.6	29.1	56.0	25.9
Dec. 31†	45.0	2.5	40.5	25.2	25.6	42.5	25.3
1939							
Jan. 14	70.0	12.5	51.4	22.5	33.5	57.5	28.8
Jan. 28†	57.0	—6.0	36.7	12.0	23.5	63.0	24.7
Feb. 11	57.5	—13.0	37.1	13.3	21.1	70.5	25.2
Feb. 25	59.5	1.5	42.4	18.5	29.9	58.0	23.9
Mar. 11	64.0	10.0	50.9	29.8	38.5	54.0	21.0
Mar. 25	93.0	18.5	68.7	34.6	49.4	74.5	34.2
Apr. 8	75.0	21.0	54.7	30.9	41.9	54.0	30.9
Apr. 22	76.5	12.0	60.0	35.4	57.1	64.5	24.7
May 6	95.0	33.5	86.5	46.9	64.8	61.5	39.5
May 20	103.0	33.5	85.0	46.3	63.2	69.5	38.7
Jun. 3	96.0	43.5	89.8	58.3	70.3	52.5	31.5
Jun. 17	94.0	53.0	84.1	59.8	70.0	41.0	24.9
Jul. 1	96.0	53.5	87.9	62.2	72.9	42.5	25.8
Jul. 15‡	104.0	56.5	95.3	66.3	78.3	47.5	29.0
Jul. 29	106.5	55.0	95.2	64.4	77.2	51.5	30.2
Aug. 12	102.0	47.0	90.3	59.7	73.2	55.0	30.6
Aug. 26	95.5	45.0	87.0	57.5	70.4	50.5	30.1
Sep. 9†	103.0	62.5	95.4	65.6	78.2	40.5	29.8
Sep. 23	106.5	37.0	95.9	57.0	74.1	69.5	38.9
Oct. 7	99.0	25.5	72.0	44.1	59.1	73.5	35.0
Oct. 21	88.0	21.0	69.1	38.2	52.3	64.0	30.8
Nov. 4	84.0	9.5	62.4	27.9	43.7	74.5	34.6

* Short period. † Record for 1 week. ‡ Record for 12 days.

TABLE 5.—Relative humidity at 0.1 meter above the surface of the ground in Station 1 (true prairie subsere).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1937							
Nov. 16	94.0	16.0	97.0	48.2	60.6	78.0	35.5
Nov. 30	91.0	23.0	82.3	47.8	66.1	68.0	34.5
Dec. 14*	88.0	26.0	74.6	43.6	60.0	62.0	34.3
Dec. 21†	88.5	42.0	85.3	51.6	73.3	46.5	33.7
1938							
Jan. 4	94.0	17.0	82.5	40.5	64.9	77.0	40.8
Jan. 18	98.0	27.5	84.5	44.8	67.7	70.5	36.8
Jan. 31	92.0	26.5	81.9	55.3	69.9	65.5	26.6
Feb. 14	100.0	21.5	87.2	49.6	71.6	78.5	35.3
Feb. 28‡	99.5	70.0	95.5	79.9	91.6	29.5	12.7
Mar. 4	100.0	30.0	96.6	57.2	83.1	70.0	39.3
Mar. 28	100.0	16.5	81.7	35.8	62.5	83.5	45.9
Apr. 11	85.5	18.0	72.8	30.5	57.7	67.5	42.2
Apr. 25	84.0	22.0	78.8	32.4	58.1	62.0	46.6
May 9	100.0	20.5	86.5	42.1	72.2	79.5	44.8
May 23	100.0	33.0	95.6	57.8	79.6	67.0	44.1
Jun. 6	96.0	35.0	92.4	50.9	74.4	61.0	41.4
Jun. 20‡	92.5	48.0	91.9	22.3	75.3	44.5	39.6
Jul. 4	100.0	37.5	87.8	52.7	73.1	62.5	37.1
Jul. 18‡	93.0	31.0	87.1	42.7	64.1	62.0	44.3
Aug. 1§	94.5	17.5	89.7	30.8	63.1	77.0	58.8
Aug. 15	92.0	19.5	81.7	31.3	57.5	72.5	50.5
Aug. 29	94.5	15.5	84.1	36.1	62.2	79.0	47.9
Sep. 12	93.0	29.5	89.2	43.8	70.0	63.5	46.1
Sep. 24†	93.5	26.5	90.7	40.0	66.9	67.0	50.7
Oct. 8	97.5	19.5	88.4	30.7	59.5	78.0	57.5
Oct. 22	94.5	18.0	84.4	33.3	59.1	76.5	51.0
Nov. 5	85.0	15.5	75.4	30.4	57.3	69.5	45.0
Nov. 19	100.0	23.0	86.6	39.2	54.1	77.0	47.3
Dec. 3	100.0	24.0	90.7	37.4	65.1	76.5	53.2
Dec. 17	100.0	22.5	88.5	41.8	67.4	77.5	46.7
Dec. 31	—	—	—	—	—	—	—
1939							
Jan. 14	96.5	19.5	87.1	41.1	68.4	77.0	47.9
Jan. 28	97.5	30.5	89.1	47.7	71.0	67.0	41.3
Feb. 11*	98.0	22.5	85.8	38.8	66.1	75.5	47.0
Feb. 25	97.5	38.0	87.8	61.4	76.1	59.5	26.4
Mar. 11	98.5	32.0	90.5	58.5	79.2	66.5	32.1
Mar. 25	95.5	15.0	86.9	31.5	63.6	80.5	55.4
Apr. 8	100.0	16.5	87.7	41.4	68.5	83.5	46.3
Apr. 22	98.5	25.5	90.9	40.2	79.9	73.0	50.8
May 6	88.0	18.0	77.2	29.1	52.1	70.0	48.1
May 20	89.0	18.0	76.0	29.4	51.3	71.0	46.6
Jun. 3	88.0	18.0	83.5	31.3	59.4	70.0	52.3
Jun. 17	88.0	14.5	84.1	36.8	61.1	73.5	48.0
Jul. 1§	88.5	22.0	86.3	34.3	62.9	66.5	52.0
Jul. 15	87.5	12.0	77.8	32.5	55.8	75.5	45.2
Jul. 29	88.0	17.0	83.3	28.1	57.2	71.0	54.9
Aug. 12	88.0	13.0	82.7	29.6	55.5	75.0	53.1
Aug. 26§	92.5	16.5	86.8	30.6	58.8	76.0	56.1
Sep. 9§	100.0	10.5	76.6	33.3	55.0	89.5	43.3
Sep. 23	83.5	14.0	63.3	19.2	39.1	69.5	44.1
Oct. 7	94.5	15.5	75.7	26.5	53.0	79.0	49.2
Oct. 21	87.5	15.0	73.8	24.1	51.9	72.5	49.7
Nov. 4	88.0	13.5	85.4	29.4	52.7	74.5	45.9

* Record for 11 days. † Short period. ‡ Record for 1 week. § Record for 12 days.

TABLE 6.—Relative humidity at 0.1 meter above the surface of the ground in Station 2 (postclimax tall grass).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1939							
Aug. 26*	98.0	22.5	91.9	38.2	77.9	75.5	42.2
Sep. 9†	95.0	19.0	81.3	34.5	64.7	76.0	46.8
Sep. 23	95.0	19.0	74.1	25.4	64.9	76.0	49.5
Oct. 7	100.0	10.5	75.4	25.5	51.2	87.0	46.4
Oct. 24	96.0	20.5	87.1	33.3	59.3	75.5	49.1
Nov. 4‡	96.0	18.0	83.2	34.3	59.2	78.0	48.9

* Record for 11 days. † Record for 1 week. ‡ Record for 12 days.

TABLE 7.—Relative humidity at 0.1 meter above the surface of the ground in Station 3 (postclimax deciduous shrub).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Aug. 1	86.0	33.0	85.1	48.5	72.9	53.0	29.5
Aug. 15*	88.0	29.0	86.4	42.3	69.0	59.0	44.2
Aug. 29	90.0	20.0	85.1	49.0	69.4	70.0	36.1
Sep. 12	88.0	38.5	84.4	60.1	76.8	49.5	24.3
Sep. 24†	87.5	31.0	85.2	47.6	72.0	56.5	37.6
Oct. 8	90.0	29.0	87.5	50.1	70.2	61.0	37.4
Oct. 22	90.0	17.5	85.5	44.4	69.0	72.5	41.0
Nov. 5	90.0	16.0	83.5	39.7	67.7	74.0	44.0
Nov. 19	100.0	22.5	90.4	41.3	71.3	77.5	49.1
Dec. 3	96.0	27.0	90.7	37.4	67.9	69.0	53.0
Dec. 17‡	95.0	25.0	89.9	37.9	67.8	70.0	51.9
Dec. 31	95.5	31.0	83.5	43.9	67.6	64.5	39.6
1939							
Jan. 14	92.0	13.5	87.7	41.9	68.7	78.5	45.5
Jan. 28‡	88.5	25.0	86.8	54.2	73.7	63.5	32.6
Feb. 11	95.5	20.0	84.9	41.5	67.5	75.5	43.4
Feb. 25	96.5	31.0	85.7	53.4	72.2	65.5	32.3
Mar. 11	93.0	26.5	86.8	55.4	74.5	66.5	31.4
Mar. 25	95.0	6.5	88.0	29.4	61.9	88.5	58.6
Apr. 8	91.0	16.0	84.8	41.2	66.1	75.0	43.6
Apr. 22	96.0	14.5	85.9	38.4	64.2	81.5	47.4
May 6	—	—	—	—	—	—	—
May 20†	95.0	19.0	92.3	30.1	64.4	76.0	62.1
Jun. 3	94.5	27.0	91.6	58.2	79.6	67.5	33.5
Jun. 17	91.0	43.0	90.1	61.1	80.0	48.0	38.9
Jul. 1*	93.0	46.0	91.6	64.3	82.5	47.0	27.3
Jul. 15†	91.0	24.0	89.5	54.8	76.4	67.0	34.7
Jul. 29†	93.0	26.0	90.1	44.2	73.5	67.0	45.9
Aug. 12§	92.0	26.5	90.4	42.1	71.6	65.5	48.3
Aug. 26	91.5	17.5	84.9	38.8	66.6	74.0	38.8
Sep. 9	93.0	25.0	89.1	37.9	66.4	68.0	51.2
Sep. 23	92.5	10.0	80.2	17.5	48.1	82.5	62.7
Oct. 7	94.0	12.0	81.3	25.8	57.1	82.0	55.5
Oct. 21	91.5	11.0	84.0	29.1	58.8	80.5	54.9
Nov. 4	95.0	12.5	86.0	32.1	61.0	82.5	53.9

* Record for 10 days. † Record for 12 days. ‡ Record for 1 week. § Record for 9 days.

TABLE 8.—Mean wind velocity (MPH) from Nov. 2, 1937 to Nov. 4, 1939 at Lincoln, Nebr.* and at 0.5 meter in Station 1 (true prairie subsere), in Station 2 (post-climax tall grass), and in Station 3 (postclimax deciduous shrub), on basis of two-week periods.

Two-week period ending	Lincoln, Nebraska	Station 1	Station 2	Station 3
1937				
Nov. 16	11.62	11.40	–	–
Nov. 30	9.81	9.13	–	–
Dec. 14	11.05	11.43	–	–
Dec. 21†	8.54	6.19	–	–
1938				
Jan. 4	9.07	9.80	–	–
Jan. 18	10.69	10.96	–	1.27
Jan. 31†	11.57	–	–	2.08
Feb. 14	10.06	–	–	1.29
Feb. 28	8.85	8.31	–	1.71
Mar. 14	9.67	10.58	–	1.56
Mar. 28	11.90	13.18	–	2.31
Apr. 11	13.96	13.92	–	3.15
Apr. 25	10.98	10.12	–	1.83
May 9	12.09	12.38	–	1.44
May 23	8.98	8.56	–	0.60
Jun. 6	8.38	–	–	0.32
Jun. 20	9.29	7.15	–	–
Jul. 4	9.87	7.50	–	0.29
Jul. 18	9.01	6.15	1.05	0.23
Aug. 1	7.32	5.30	0.77	0.23
Aug. 15	11.25	8.49	–	0.36
Aug. 29	9.39	7.13	–	0.36
Sep. 12	8.32	6.83	–	0.11
Sep. 24†	7.11	5.41	–	0.41
Oct. 8	8.13	6.29	1.24	0.15
Oct. 22	10.85	8.91	1.90	0.38
Nov. 5	9.79	8.43	1.95	0.69
Nov. 19	10.80	9.27	1.70	0.36
Dec. 3	8.58	–	–	–
Dec. 17	9.56	–	–	–
Dec. 31	10.48	9.26	1.61	1.15
1939				
Jan. 14	8.68	8.20	1.31	0.77
Jan. 28	10.26	8.78	1.82	1.16
Feb. 11	11.57	–	1.85	1.72
Feb. 25	11.07	11.02	–	1.95
Mar. 11	10.07	10.33	–	1.71
Mar. 25	10.49	12.82	2.92	1.48
Apr. 8	10.61	–	3.31	2.12
Apr. 22	12.25	–	3.91	2.45
May 6	11.17	9.10	–	1.39
May 20	9.22	8.58	2.91	0.88
Jun. 3	9.10	8.63	2.41	0.20
Jun. 17	10.21	9.06	3.09	0.30
Jul. 1	8.52	7.64	1.84	0.15
Jul. 15	8.91	7.74	1.42	0.05
Jul. 29	8.39	7.71	1.08	0.17
Aug. 12	9.02	8.54	–	0.10
Aug. 26	7.65	7.07	–	0.18
Sep. 9	10.59	9.72	–	0.42
Sep. 23	10.45	8.34	2.68	1.06
Oct. 7	11.09	8.46	2.73	0.64
Oct. 21	9.61	7.12	2.27	0.77
Nov. 4	8.91	6.03	1.62	1.19

* Data courtesy of U. S. Weather Bureau, Lincoln, Nebraska. † Short period.

TABLE 9.—Water content of soil, expressed as per cent in excess of the hygroscopic coefficient at a depth of 0 to 0.1 meter, of true prairie subsere (Station 1), of postclimax tall grass (Station 2, ravine), and of postclimax deciduous shrub (Station 3, ravine).

Date	Station 1	Station 2	Station 3
1938			
Jan. 13	17.1	41.5	—
Feb. 5	20.8	55.4	45.4
Mar. 21	29.5	45.9	41.1
Apr. 4	23.5	—	38.6
Apr. 18	34.5	35.3	57.2
May 16	31.0	37.4	46.1
Jun. 21	32.2	32.8	42.1
Jul. 2	29.5	49.2	42.2
Jul. 19	6.5	21.4	20.6
Jul. 26	6.9	17.4	20.0
Aug. 12	5.9	15.2	14.4
Oct. 29	8.4	22.0	16.0
Nov. 5	23.0	35.4	45.6
Nov. 26	13.8	26.5	26.3
1939			
Jan. 7	12.3	19.5	46.6
Mar. 12	29.1	52.4	60.4
Means	20.25	33.82	37.48

TABLE 10.—Soil temperature in degrees F. at 0.1 meter below soil surface in Station 1 (true prairie subsere).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1937							
Nov. 16	57.0	41.0	54.2	48.4	50.7	16.0	5.8
Nov. 30*	44.0	36.0	40.5	37.5	38.3	8.0	3.0
Dec. 14	43.5	31.0	36.5	34.2	35.7	12.5	2.3
Dec. 21†	36.0	33.0	35.4	34.1	34.7	3.0	1.3
1938							
Jan. 4*	36.0	33.0	35.6	33.9	34.8	3.0	1.7
Jan. 18	36.0	30.5	35.1	32.3	31.6	5.5	2.8
Jan. 31‡	38.5	33.0	36.2	34.0	35.4	5.5	2.2
Feb. 14	42.0	22.5	32.6	31.0	32.2	19.5	1.6
Feb. 28	34.5	32.5	34.0	33.6	34.0	2.0	0.2
Mar. 14	50.5	34.0	41.0	37.6	39.2	16.5	3.4
Mar. 28	58.0	40.0	50.4	43.5	46.7	18.0	6.8
Apr. 11	56.0	36.0	48.5	40.9	43.4	20.0	6.6
Apr. 25	64.0	40.0	56.9	48.5	55.6	24.0	8.3
May 9	67.0	38.0	58.6	48.8	53.0	29.0	9.8
May 23	71.0	50.5	64.7	58.0	62.1	20.5	6.6
Jun. 6	76.0	58.0	72.4	65.4	68.7	18.0	7.0
Jun. 20	81.0	65.0	76.5	71.0	74.0	16.0	5.4
Jul. 4	82.0	67.0	77.3	71.8	74.9	15.0	4.5
Jul. 18*	83.0	73.0	80.7	75.5	77.5	10.0	5.2
Aug. 1‡	85.5	76.0	82.8	77.3	79.8	9.5	5.5
Aug. 15	90.0	78.0	87.7	81.5	80.3	12.0	6.2
Aug. 29	89.0	74.5	84.6	80.0	81.5	14.5	5.9
Sep. 12‡	86.5	76.5	81.8	77.7	80.4	10.0	4.6
Sep. 24†‡	79.5	60.5	71.3	65.0	67.0	19.0	6.3
Oct. 8	72.5	64.5	71.0	66.2	68.5	8.0	4.7
Oct. 22	71.0	53.0	64.5	59.6	61.7	18.0	4.8
Nov. 5	60.5	47.0	56.6	51.7	53.5	13.5	4.9

* Record for 11 days. † Short period. ‡ Record for 1 week.

TABLE 11.—Soil temperature in degrees F. at 0.1 meter below soil surface in Station 2 (postclimax tall grass).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Jan. 18	35.0	30.0	33.1	31.1	32.2	5.0	1.9
Jan. 31	35.0	29.0	32.7	31.3	32.0	6.0	1.3
Feb. 14	34.5	28.0	31.6	30.0	30.6	6.5	1.6
Feb. 28	35.0	32.0	33.9	32.9	33.4	3.0	1.0
Mar. 14	41.5	32.0	36.5	34.2	35.7	9.5	2.3
Mar. 28	51.5	41.5	47.2	44.2	45.7	10.0	3.1
Apr. 11	49.0	39.5	45.0	42.6	43.9	9.5	1.7
Apr. 25	55.0	43.0	52.4	48.7	51.0	12.0	3.6
May 9	60.0	47.0	55.6	52.4	54.0	13.0	3.2
May 23	57.0	48.0	54.5	51.9	53.4	9.0	2.5
Jun. 6	61.0	51.0	58.5	55.2	56.9	10.0	3.3
Jun. 20	63.0	55.5	60.6	57.8	59.3	7.5	2.9
Jul. 4	75.0	70.0	72.4	69.9	71.3	5.0	2.4
Jul. 18	74.0	67.5	72.5	69.9	72.1	6.5	2.7
Aug. 1*	71.5	61.0	70.6	67.8	70.2	4.5	2.7
Aug. 15*	73.0	66.0	71.1	78.0	72.0	7.0	2.8
Aug. 29	71.0	65.0	69.4	66.7	71.1	6.0	2.7
Sep. 12	70.5	64.0	68.4	66.2	71.4	6.5	2.1
Sep. 24†	68.0	55.0	63.3	60.1	67.0	13.0	3.2
Oct. 8	62.0	56.5	61.3	58.1	65.9	5.5	3.1
Oct. 22‡	60.0	51.0	58.0	55.5	63.8	9.0	2.1
Nov. 5	56.0	46.5	63.0	45.7	59.1	9.5	7.2
Nov. 19	50.5	42.5	47.2	45.6	47.0	8.0	2.4
Dec. 3	48.0	38.5	43.6	41.7	42.8	9.5	1.9
Dec. 17	46.0	40.0	43.9	42.0	43.2	6.0	1.6
Dec. 31	42.0	38.5	41.1	39.5	40.5	3.5	1.6
1939							
Jan. 14	45.0	38.0	42.1	40.4	41.3	7.0	1.7
Jan. 28†	42.5	38.0	41.1	39.9	40.7	4.5	1.3
Feb. 11	37.0	33.0	35.4	33.9	34.9	4.0	1.3
Feb. 25*	36.0	33.0	35.0	33.8	34.6	3.0	1.2
Mar. 11	34.5	32.5	34.3	32.6	33.9	2.0	1.7
Mar. 25‡	44.0	30.5	36.3	33.9	35.3	13.5	2.4
Apr. 8	45.5	36.5	42.0	39.5	40.9	9.0	2.5
Apr. 22	46.0	37.0	43.4	40.9	42.2	9.0	2.4
May 6	52.0	45.0	49.7	46.2	48.1	7.0	3.4

* Record for 1 week. † Record for 12 days. ‡ Record for 11 days.

TABLE 12.—Soil temperature in degrees F. at 0.1 meter below soil surface in Station 3 (postclimax deciduous shrub).

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Max. Range	Mean Range
1938							
Jan. 18	30.0	24.0	29.2	28.0	24.9	6.0	1.2
Jan. 31	32.0	26.0	29.0	27.0	30.7	6.0	2.0
Feb. 14	31.0	24.0	28.7	25.9	29.2	7.0	2.9
Feb. 28	31.5	30.0	31.3	30.3	30.2	1.5	2.0
Mar. 14	40.0	30.5	35.6	32.3	31.9	9.5	3.5
Mar. 28	50.5	37.0	44.6	41.1	42.7	13.5	3.5
Apr. 11	48.5	35.0	41.9	38.7	40.2	13.5	3.2
Apr. 25	58.0	41.0	54.1	50.2	51.9	17.0	3.9
May 9	64.5	48.5	59.2	51.5	57.5	16.0	7.7
May 23	62.0	51.5	57.9	55.2	56.9	11.5	2.7

TABLE 12.—(*Continued*)

Two-week period ending	Abs. Max.	Abs. Min.	Mean Max.	Mean Min.	Mean	Range Max.	Mean Range
Jun. 6	65.5	54.0	62.2	58.9	60.7	11.5	3.4
Jun. 20	68.5	60.0	65.6	63.0	64.3	8.5	2.6
Jul. 4	73.5	63.5	69.8	67.7	68.7	10.0	2.0
Jul. 18	74.0	65.5	71.8	69.0	70.5	8.5	2.8
Aug. 1	70.5	64.5	69.5	66.7	67.9	6.0	2.8
Aug. 15	73.5	65.5	71.5	69.5	70.5	8.0	2.1
Aug. 29	73.0	66.0	70.6	68.2	69.5	7.0	2.3
Sep. 12	73.5	66.5	70.8	69.1	70.3	7.0	1.8
Sep. 24*	71.0	55.0	53.6	60.9	62.5	16.0	2.7
Oct. 8	64.0	59.0	62.7	60.3	61.5	5.0	2.5
Oct. 22	63.5	52.0	59.9	57.7	58.9	11.5	2.2
Nov. 5	57.0	47.0	52.0	49.9	51.1	10.0	2.1
Nov. 19	48.0	39.5	43.1	41.5	42.4	8.5	1.6
Dec. 3	42.5	32.0	37.6	34.4	34.9	10.5	5.7
Dec. 17	36.5	32.0	34.7	32.7	34.1	4.5	2.0
Dec. 31	32.0	28.5	32.0	29.8	30.9	3.5	2.3
1939							
Jan. 14	32.0	29.5	31.7	30.5	30.8	2.5	1.3
Jan. 28	32.0	30.0	31.8	30.3	30.5	2.0	1.5
Feb. 11	31.5	27.5	30.7	29.4	30.2	4.0	1.3

* Record for 12 days.

TABLE 13.—Number of cubic centimeters evaporated from porous cup atmometers (reduced to standard) in the aerial strata studied in Station 1 (true prairie subsere), in Station 2 (postclimax tall grass), and in Station 3 (postclimax deciduous shrub).

Two-week period ending	Station 1 0.35 meter	Station 2 0.35 meter	Station 3 0.35 meter	Station 3 2.0 meters
1938				
Jul. 4	136.68*	86.52*	64.60*	130.78
Jul. 18	159.27	97.43	78.17	151.86
Aug. 1	200.70	114.48	84.31	155.77
Aug. 15	372.35	186.77	149.59	260.14
Aug. 29	234.19	120.12	122.02	209.15
Sep. 12	136.40*	—	78.17	149.52

* Based on record for 1 week.

TABLE 14.—Light intensity in foot candles at surface of the ground in true prairie subsere (Station 1), postclimax tall grass (Station 2), and postclimax deciduous shrub (Station 3). (Average of 10 readings at intervals of 1.0 meter along a random transect, 11:30 A.M. to 12:30 P.M. on July 1, 1938.)

Station 1	Station 2	Station 3
3890.0	1190.7	750.5

TABLE 15.—Analysis of soil samples (8 replicate) from each station.

	Station	Organic matter %	Volatile matter %	Nitrogen %	Hygroscopic coefficient %	pH
Prairie subsere	(1)	4.8	6.3	0.207	7.6	6.4
Tall grass	(2)	5.6	7.2	0.226	9.6	6.6
Shrub	(3)	8.6	10.0	0.350	12.2	6.8

TABLE 16.—Summary of seasonal and annual means of aerial factors and of soil temperature and moisture, and range of soil temperature as determined during the period of study in true prairie subsere (Station 1), postclimax tall grass (Station 2), and postclimax deciduous shrub (Station 3).

	Prevernal-vernal			Estival			Autumnal			Hiemal			Annual		
	Station			Station			Station			Station			Station		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Aerial temperature (°F.)															
Mean	53.8	52.6	55.4	74.8	72.8	72.5	71.9	69.9	68.6	33.5	32.3	32.6	54.2	53.5	53.6
Mean range	21.6	27.1	29.2	25.2	31.1	27.6	29.8	34.7	29.9	21.1	28.3	25.8	23.9	33.3	27.7
Relative humidity (%)															
Mean	63.8	—	64.9	64.6	—	77.5	57.4	63.6	66.2	67.8	—	69.3	64.1	—	69.3
Mean range	46.2	—	51.0	47.3	—	33.3	49.9	46.8	44.3	39.2	—	44.6	44.3	47.1	43.0
Wind velocity															
Mean	10.44	3.38	1.73	7.38	1.66	0.215	7.69	2.16	0.411	9.71	1.85	1.40	8.82	2.06	0.94
Evaporation rate															
Mean (herb)	—	—	—	166.55	99.46	75.69	247.64	153.44	116.59	—	—	—	206.60	121.60	96.16
(shrub)	—	—	—	—	—	146.13	—	—	206.37	—	—	—	—	—	179.20
Soil temperature (°F.)															
Mean	53.5	47.6	51.6	75.0	65.9	66.4	73.2	68.5	65.2	38.9	39.0	33.9	55.3	52.8	49.7
Mean range	7.8	2.7	4.4	5.5	2.8	2.7	5.4	2.7	2.2	3.0	2.1	2.3	4.7	2.4	2.7
Abs. max.	71.0	60.0	64.5	85.5	75.0	74.0	90.0	73.0	83.5	60.5	56.0	57.0	90.0	75.0	74.0
Abs. min.	36.0	39.5	35.0	65.0	51.0	54.0	53.0	51.0	52.0	22.5	28.0	24.0	22.5	28.0	24.0
Max. range	35.0	20.5	29.5	20.0	24.0	20.0	37.0	22.0	21.5	38.0	28.0	33.0	68.5	47.0	50.0
Soil moisture															
Mean	29.7	36.3	47.3	18.8	30.2	31.8	5.9	15.2	14.4	19.2	37.3	40.2	20.25	33.82	37.48

TABLE 17.—Daily and nightly means of temperature and relative humidity in Station 1 (true prairie subsere) at times of collection (see Table 32) during period of day-night studies.

Date 1938	Temperature °F. Day A.M.	Day P.M.	Night P.M.	Night A.M.	Relative Humidity % Day A.M.	Day P.M.	Night P.M.	Night A.M.
Jun. 12	—	79.3	—	—	—	—	—	—
17	76.2	79.8	—	—	73.4	55.0	—	—
18	—	—	73.7	—	—	—	77.0	—
19	—	—	—	68.2	—	—	—	90.5
21	—	82.2	—	—	—	67.0	—	—
23	78.0	91.0	80.1	—	79.5	63.0	82.5	—
25	68.2	—	—	—	87.9	—	—	—
28	68.6	—	—	—	61.5	—	—	—
29	—	—	80.0	—	—	—	79.5	—
30	—	91.0	—	75.5	—	49.8	—	85.5
Jul. 1	89.7	99.0	—	—	68.1	46.7	—	—
2	—	90.3	—	—	—	52.0	—	—
5	—	90.3×	—	—	—	42.4	—	—
7	—	81.3×	70.8×	—	—	49.8	72.7	—
8	71.2	—	—	—	61.6×	—	—	—
9	76.8	87.7×	—	—	66.5	46.0×	—	—
18	—	—	71.0	—	—	—	75.3	—
19	—	—	—	65.3	—	—	—	85.5
21	—	—	71.7	—	—	—	79.8	—
22	76.5	91.0	—	—	59.0	28.9	—	—
26	—	86.7	—	—	—	52.2	—	—
28	—	86.0	74.1	—	—	58.1	83.3	—
29	81.4	—	—	—	51.5	—	—	—
Aug. 1	—	98.2	—	—	—	23.9	—	—
2	86.2	—	—	—	48.2	—	—	—
3	—	—	71.7	—	—	—	67.0	—
4	—	—	81.0	—	—	—	65.2	—
5	93.2	109.0	—	—	45.7	26.9	—	—
6	—	—	—	76.5	—	—	—	71.0
10	—	—	60.8	—	—	—	81.5	—
11	—	—	—	52.5	—	—	—	89.7
12	—	87.0	—	—	—	21.7	—	—
15	—	77.0	—	—	—	59.2	—	—
22	—	94.2	—	—	—	24.0	—	—
25	—	81.7	—	—	—	46.7	—	—
29	75.0	—	—	—	60.3	—	—	—
Sep. 3	—	—	58.0	—	—	—	85.8	—
5	—	76.3	—	—	—	74.2	—	—
7	80.3	—	—	—	52.6	—	—	—
12	63.0	—	—	—	81.7	—	—	—
18	—	64.0×	—	—	—	40.0×	—	—
Oct. 1	66.6	—	—	—	73.0	—	—	—
7	—	—	70.5	—	—	—	43.8	—
8	67.2	—	—	—	69.2	—	—	—
15	59.0	—	—	—	71.0	—	—	—
21	—	—	60.8	—	—	—	45.0	—
22	43.5	—	—	—	64.3	—	—	—
29	45.8	—	—					
Av. of means	71.8	86.8	71.1	67.6	65.5	46.3	72.2	84.4

× Interpolated.

TABLE 18.—Daily and nightly means of temperature* in Station 2 (postclimax tall grass) at times of collection (see Table 32) during period of day-night studies.

Date	Temperature °F. Day A.M.	Day P.M.	Night P.M.	Night A.M.
1938				
Jun. 12	—	78.7	—	—
17	81.3	81.3	—	—
18	—	—	74.0	—
21	—	79.4	—	—
23	83.0	89.5	75.7	—
25	69.0	—	—	—
28	67.7	—	—	—
29	—	—	76.5	—
30	—	—	—	70.2
Jul. 1	91.0	82.0	—	—
5	—	92.3	—	—
7	—	81.0	64.2	—
8	88.5	—	—	—
15	—	88.3	—	—
18	—	—	74.0	—
19	—	—	—	57.8
21	—	—	68.2	—
22	—	91.2	—	—
28	—	83.3	68.5	—
29	89.4	—	—	—
Aug. 3	—	—	66.3	—
4	—	—	78.8	—
5	100.2	102.3	—	—
6	—	—	—	75.0
10	—	—	64.3	—
11	—	—	—	51.7
12	—	94.0	—	—
15	—	93.5	—	—
Sep. 3	—	—	61.5	—
5	—	‡	—	—
9	93.6	—	—	—
18	—	63.0	—	—
Oct. 1	62.5†	—	—	—
7	—	—	59.7	—
8	85.3	—	—	—
15	81.0	—	—	—
21	—	—	52.5	—
22	‡	—	—	—
29	61.2	—	—	—
Av. of means	81.0	85.0	68.0	63.7

* Relative humidity records were not secured in this station in 1938. † Interpolated.
‡ No record.

TABLE 19.—Daily and nightly means of temperature and relative humidity in Station 3 (postclimax deciduous shrub) at times of collection (see Table 32) during period of day-night studies.

	Temperature °F.				Relative Humidity %			
	Day		Night		Day		Night	
Date	A.M.	P.M.	P.M.	A.M.	A.M.	P.M.	P.M.	A.M.
1938								
Jun. 12	—	81.7	—	—	—	×	—	—
17	76.5	81.7	—	—	×	×	—	—
18	—	—	68.0	—	—	—	×	—
21	—	84.3	—	—	—	×	—	—
23	82.3	—	—	—	×	—	—	—
25	83.8	—	—	—	×	—	—	—
28	73.2	—	—	—	×	—	—	—
Jul. 1	89.5	90.5	—	—	×	×	—	—
7	—	85.8	—	—	—	×	—	—
15	—	88.7	—	—	—	61.5	—	—
21	—	—	52.9	—	—	—	84.3	—
22	—	83.8	—	—	—	33.4	—	—
28	—	78.2	—	—	—	75.1	—	—
Aug. 2	80.7	—	—	—	67.1	—	—	—
3	—	—	65.5	—	—	—	82.2	—
5	—	98.8	—	—	—	44.5	—	—
6	—	—	—	72.2	—	—	—	79.6
11	—	—	—	54.4	—	—	—	85.0
25	—	84.3	—	—	—	54.5	—	—
Oct. 7	—	—	56.5	—	—	—	80.2	—
18	—	58.7	—	—	—	48.9	—	—
22	43.0	—	—	—	65.0	—	—	—
29	45.3	—	—	—	72.0	—	—	—
Av. of means	71.9	83.3	60.7	63.3	68.0	53.0	82.2	82.3

× No record.

TABLE 20.—Mean day and night wind velocities (MPH), at Lincoln, Nebraska,* June 12 (sunrise) to October 29 (sunrise), 1938, on basis of two-week periods.

Day (Sunrise to sunset)		Night (Sunset to sunrise)	
Two-week period	Mean MPH	Two-week period	
Jun. 12-19†	10.12	Jun. 12-20†	10.17
Jun. 20-Jul. 3	10.06	Jun. 20-Jul. 4	9.30
Jul. 4-17	9.86	Jul. 4-18	7.65
Jul. 18-31	8.12	Jul. 18-Aug. 1	6.00
Aug. 1-14	12.49	Aug. 1-15	9.59
Aug. 15-28	10.12	Aug. 15-29	12.14
Aug. 29-Sep. 11	8.84	Aug. 29-Sep. 12	7.10
Sep. 12-23	8.17	Sep. 12-24	5.74
Sep. 24-Oct. 7	8.71	Sep. 24-Oct. 8	5.19
Oct. 8-21	11.98	Oct. 8-22	10.25
Oct. 22-28†	11.12	Oct. 22-29	7.49
Av. of means	9.96		8.25

* Wind velocity data courtesy U. S. Weather Bureau, Lincoln, Nebraska. † Record for 1 week.

TABLE 21.—Average wind velocities (MPH) at Lincoln, Nebraska* during the hours specified of those days and nights on which sweep collections were made. (See Table 32.)

	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-3 A.M.
Av. MPH	9.56	10.18	7.96	9.53

* Wind velocity data courtesy U. S. Weather Bureau, Lincoln, Nebraska.

TABLE 22.—Average numbers of invertebrates per unit collection taken by sweep net method of sampling invertebrate populations (187 unit collections, day sweeps) in the herb stratum of true prairie subsere (Station 1 and substations), postclimax tall grass (Station 2 and substation, ravine), and postclimax deciduous shrub (Station 3 and substations, ravine), on basis of two-week periods.

Population breakdown	Number of specimens collected	Station	Station totals	Average numbers per unit collection for two-week period ending																											Seasonal averages per unit collection				
				1937		1938																		1939											
				Nov.		Mar.		Apr.		May		Jun.		Jul.			Aug.		Sep.			Oct.		Nov.		Dec.	Jan.	Feb.	Mar.						
				16	28	11	25	9	23	6	20	4	18	1	15	29	12	24*	8	22	5	19	3	14	11	25	Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal
Araneida (spiders)	2,455	1	1,037	0	0	0	2—	3—	2—	9	18	1	15	23	27	29	15	38	16	8	1—	0	0	0	1	1—	0	1+	18	25	1—
		2	510	0	1—	1—	1—	5—	4—	9	9	7	14	32	25	43	17	24	23	7	4	3—	2—	0	0	1—	1—	2+	15	20	2—
		3	908	5—	5	2	6	14	35	20	21	16	44	45	45	69	x	32	26	24	19	16	5—	2	0	3—	5—	14	25	37	7
Orthoptera (grasshoppers, walking sticks, etc.)	3,716	1	2,044	0	0	0	1	15	75	60	52	51	31	83	63	25	13	8	1	2	1—	0	0	0	0	2—	2+	5	44	29	1—
		2	1,186	0	1	1	1	20	41	30	27	41	28	33	55	54	3	6	0	1—	1—	0	0	0	0	0	0	23	41	21	1—
		3	486	3	1	1—	1	11	8	20	54	18	21	9	12	14	x	5—	2	1	1—	1—	0	0	0	0	1—	16	21	6	1—
Homoptera (leafhoppers, aphids, etc.)	12,748	1	5,343	4—	1—	0	2—	14	15	154	275	143	112	118	56	33	75	137	124	88	7	7	2	1	1	12	3—	8	149	67	4—
		2	1,825	2—	1—	0	0	15	76	63	37	52	58	93	67	28	42	11	46	38	4+	4—	2—	1	0	1	1+	23	59	44	2+
		3	5,580	4+	1	2	10	9	56	65	114	140	151	281	242	391	x	81	350	549	230	55	5	5	7	36	3+	32	146	311	49
Hemiptera (true bugs)	2,990	1	605	3+	3—	0	1	3	6	5—	18	21	29	12	7	3	2—	10	6	4—	1—	0	0	0	0	1—	3	3—	19	5	1—
		2	1,121	34	11	3—	3—	62	35	34	13	8	11	10	8	2	6	5	20	116	23	5	3—	0	0	5	26	25	13	37	7
		3	1,264	58	26	2—	2—	20	49	46	24	15	14	18	5	9	x	8	73	149	60	14	1	0	0	1	44	18	20	51	12
Diptera (flies)	9,986	1	1,795	1—21		2	4	20	19	40	76	38	40	37	5	14	61	53	31	27	2—	1—	1	0	0	3	7	11	43	26	1+
		2	2,128	2—	2—	13	6	35	95	89	36	53	74	88	46	7	80	66	60	42	8	2	2—	3—	0	2—	2—	37	64	51	3—
		3	6,063	8	19	8	18	67	107	98	118	98	160	155	145	75	x	24	557	1282	115	22	2	2+	0	4—	11	50	118	442	23
Coleoptera (beetles)	4,674	1	2,913	1—	6	0	4—	4	0	26	237	103	57	91	21	18	8	10	18	27	1—	0	1—	0	0	1—	2+	2—	102	17	1—
		2	812	2+	2	2—	3	20	11	36	50	26	24	24	8	52	7	2	17	10	2—	1—	2—	1	0	1—	2+	9	30	13	1—
		3	949	2	3—	2+	11	20	12	55	93	29	89	25	8	22	x	8	32	24	4	5	0	0	0	1—	2+	11	46	17	1+
Winged Hymenoptera (bees, wasps)	2,979	1	883	0	0	0	1—	4—	2—	47	31	26	33	26	7	4	12	8	4	5—	1—	0	0	0	0	1—	0	1+	30	7	1—
		2	857	2—	7	1—	0	9	10	32	9	18	30	44	47	14	12	10	33	31	1	1—	1—	0	0	1—	3+	5	25	29	1—
		3	1,239	6	0	1	4—	19	18	23	26	24	54	43	24	40	x	6	70	220	30	3	0	0	0	0	4—	10	31	76	5
Formicidae (ants)	3,372	1	1,166	0	0	0	0	5	4—	25	30	22	28	27	23	44	6	10	5	2	0	0	0	0	0	0	0	2+	26	22	0
		2	703	1—	0	0	0	15	27	46	33	24	9	5	9	155	7	5	1	2—	0	1—	0	0	0	0	1—	11	22	19	1—
		3	1,503	0	1—	0	9	53	61	50	72	51	50	25	11	8	x	11	75	121	48	14	0	0	0	0	1—	30	51	46	9
Other invertebrates†	272	1	65	0	0	0	0	0	0	0	5—	2	1—	1—	1—	1+	1	2+	1	0	0	0	0	0	0	0	0	0	2—	1+	0
		2	80	1—	3	1—	1—	1—	1—	0	3—	3+	1	1—	4+	0	3	0	6	1+	0	0	0	0	0	1—	1+	1—	2+	3—	1—
		3	127	1—	12	1—	1—	3—	0	0	3+	4	4	4	1	4	x	2—	9	3	2—	2—	0	0	0	5—	4+	1	3+	3	2—
Larvae‡	1,226	1	527	0	0	0	1	3—	2—	17	11	10	4	11	8	4	9	46	11	9	0	0	0	0	0	0	0	1+	10	12	0
		2	250	1—	1—	1—	1	5	5—	16	19	5	2	7	6	5	2—	2	11	6	1+	2	0	1—	0	1—	1—	3—	8	5	1+
		3	449	0	1	1+	3—	21	56	19	22	20	7	2	4—	3	x	2	8	9	1	1	1—	0	1	0	1—	20	16	5	1—
Total population (as studied)	44,418	1	16,378	11	31	3	14	65	56	342	756	434	354	428	218	175	200	323	217	170	11	8	4	1	2	10	17	34	452	210	6
		2	9,472	42	26	19	14	182	337	384	258	237	251	335	276	360	177	131	217	255	44	18	9	5	0	9	37	138	275	241	16
		3	18,568	77	68	19	62	293	434	405	489	415	596	595	495	635	x	177	1202	2382	507	134	14	10	8	25	74	202	477	933	107

* Short period. † Mollusca (snails), Ixodoidea (ticks), Phalangida (harvestmen), Odonata (dragon-flies and damsel-flies), Ephemerida (May-flies), Neuroptera (lacewing flies), and Lepidoptera (butterflies and moths). ‡ Larvae of Neuroptera, Lepidoptera, and Coleoptera. x No collection.

TABLE 23.—Average numbers of invertebrates per unit collection taken by sweep net method of sampling invertebrate populations (24 unit

TABLE 23.—Average numbers of invertebrates per unit collection taken by sweep net method of sampling invertebrate populations (24 unit collections, day sweeps) in the shrub stratum (1-2 meters) of postclimax deciduous shrub of ravine in true prairie subsere (Station 3 and substations), on basis of two-week periods.

Population Breakdown	Number of specimens collected*	Average numbers for two-week period ending											Seasonal averages per unit collection				
		1938 Apr. 25	May 9	May 23	Jun. 6	Jun. 20	Jul. 4	Jul. 18	Aug. 1	Aug. 15	Aug. 29	Sep. 24	1939 Mar. 25	Prevernal-vernal	Estival	Autumnal	(Late) Hiemal†
Araneida (spiders)	119	23	28	25	28	30	28	8	33	45	30	0	5	25	26	25	5
Orthoptera (grasshoppers, walking sticks, etc.)	71	0	0	0	3—	5	29	40	25	35	25	0	0	0	21	20	0
Homoptera (leafhoppers, aphids, etc.)	519	10	30	15	55	63	156	133	355	215	215	0	0	18	147	143	0
Hemiptera (true bugs)	31	15	10	8	3—	5	2	18	10	0	5	0	0	11	6	2—	0
Diptera (flies)	716	228	365	178	98	143	123	145	193	50	75	0	0	257	137	42	0
Coleoptera (beetles)	360	220	188	75	98	103	31	38	15	15	45	0	10	161	55	20	10
Winged Hymenoptera (bees and wasps)	555	120	175	38	75	165	145	198	110	85	40	0	0	111	142	42	0
Formicidae (ants)	241	73	133	65	108	53	22	33	33	10	40	0	0	90	44	17	0
Other Orders‡	28	3—	5	3—	0	7	8	0	3—	5	0	0	50	3+	5—	2—	50
Larvae§	142	85	130	28	20	25	13	13	0	5	15	0	0	81	15	7	0
Total Population (as studied)	2782	775	1063	433	485	600	557	623	775	465	490	0	65	757	596	318	65

* Unit collections were comprised of only 10 sweeps in this stratum; actual population values so derived are multiplied by 5 for comparison with unit collections in the herb stratum. † Based on 1 collection. ‡ Lepidoptera (butterflies and moths), Neuroptera (lacewing flies), and Ephemerida (May-flies). § Larvae of Lepidoptera and Coleoptera.

TABLE 24.—Average numbers of invertebrates per unit collection taken by enclosed quadrat method of sampling invertebrate populations (102 unit collections) in the litter stratum of true prairie subsere (Station 1 and substations), postclimax tall grass (Station 2 and substation, ravine) and postclimax deciduous shrub (Station 3 and substations, ravine).

Population breakdown	No. of specimens collected	Station	Station totals	Seasonal averages					
				Late Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal	Yearly averages
		1	7	1—	1—	0	0	0	1—
Mollusca	263	2	4	0	0	0	1	0	1—
(snails)		3	252	4+	8	18	8	0	7
		1	59	1—	3—	4+	0	1—	2—
Annelida	941	2	212	4+	13	19	0	1	7
(earthworms)		3	670	10	62	4	0	15	19
		1	64	3—	1	1—	1—	3+	2—
Araneida	560	2	162	3—	4	2+	2—	10	5
(spiders)		3	334	2—	3—	2+	11	20	9
		1	46	6	1—	1—	1—	2—	1+
Hemiptera	880	2	351	2+	8	1—	6	25	12
(true bugs)		3	483	9	4—	1—	10	32	13
		1	181	3+	8	7	3—	4—	5
Coleoptera	1229	2	567	10	8	5	4—	40	19
(beetles)		3	481	8	8	6	17	21	13
		1	77	3—	5	3—	0	1—	2
Formicidae	467	2	165	1—	17	7	1	1—	6
(ants)		3	225	11	11	7	1+	4—	6
		1	58	2—	2—	1—	3—	1+	2+
Other	348	2	102	15	2+	1	1	2—	3+
Arthropods*		3	188	1—	2+	1+	5+	9	5
		1	38	1—	3	1—	1—	1—	1
Larvae†	294	2	84	1—	5—	1	4—	3	3—
		3	172	2+	4+	1+	4+	9	5—
		1	530	17	22	16	6	11	14
Total population	4982	2	1647	35	57	34	19	81	55
(as studied)		3	2805	89	101	46	56	111	78

* Myriapoda (centipedes and millipedes), Chelonethida (pseudoscorpions), Orthoptera (grasshoppers and crickets), Isoptera (termites), Homoptera (leafhoppers), Diptera (flies), winged Hymenoptera (bees and wasps), and undetermined pupae.

† Larvae of Neuroptera (lacewing flies), Lepidoptera (butterflies and moths), and Coleoptera.

TABLE 25.—Average numbers of invertebrates per unit collection taken by enclosed quadrat and soil washer method of sampling invertebrate populations (63 unit collections) in the soil stratum (10 cms.) of true prairie subsere (Station 1 and substations), postclimax tall grass (Station 2 and substation, ravine), and postclimax deciduous shrub (Station 3 and substations, ravine), on basis of seasons.

Population breakdown	No. of specimens collected	Station	Station totals	Seasonal averages: Prevernal-vernal	Estival	Autumnal	Hiemal	Yearly averages
		1	2	0	1—	0	0	1—
Mollusca	67	2	0	0	0	0	0	0
(snails)		3	65	5—	4—	1	3+	3+
		1	21	3—	1	0	0	1—
Annelida	47	2	21	2—	2	2—	1—	1+
(earthworms)		3	5	1—	1—	0	0	1—
Araneida	21	2	2	1—	0	0	1—	1—
(spiders)		3	14	0	0	1—	1—	1—
		1	0	0	0	0	0	0
Hemiptera	73	2	2	0	0	1—	1—	1—
(true bugs)		3	71	1—	1—	12	8	4—
		1	71	2+	3—	4	3+	3
Coleoptera	277	2	88	6	2+	1	6	5—
(beetles)		3	118	1	2+	12	9	6—
		1	3	0	0	1—	1—	1—
Formicidae	24	2	4	0	0	1—	1—	1—
(ants)		3	17	1—	3—	1—	1—	1—
		1	14	0	1—	0	1—	1—
Other	37	2	4	1—	1—	0	1—	1—
Arthropods*		3	19	1—	1—	1	1	1—
		1	95	2—	3+	13	3—	4
Larvae†	143	2	13	1—	1	0	1—	1—
		3	35	2+	5—	1	1—	2—
Total		1	211	7	8	17	7	9
population	689	2	134	9	6	4	8	7
(as studied)		3	344	10	14	29	19	17

* Myriapoda (centipedes and millipedes), Isopoda (sow-bugs), Orthoptera (grasshoppers and crickets), Diptera (flies), winged Hymenoptera (bees and wasps), and undetermined pupae.

† Larvae of Neuroptera (lacewing flies), Lepidoptera (butterflies and moths), and Coleoptera.

TABLE 26.—Total numbers per two-week periods and seasonal averages of invertebrates taken by alcohol pitfall at the ground surface (76 unit collections) in true prairie subsere (Station 1), postclimax tall grass (Station 2, ravine), and postclimax deciduous shrub (Station 3, ravine), April 8 to November 4, 1939. (Leafhoppers, true flies, bees, wasps, lacewing flies, butterflies, and moths omitted from pitfall studies.)

Population breakdown	No. of specimens collected	Station	Station totals	Total numbers for two-week period ending: 1939 Apr 22	May 6	May 20	Jun. 3	Jun. 17	Jul. 1	Jul. 15	Jul. 29	Aug. 12	Aug. 26	Sep. 9	Sep. 23	Oct. 7	Oct. 21	Nov. 4	Seasonal average per unit collection: Vernal	Estival	Autumnal	Hiemal
		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca	64	2	9	×	×	×	0	0	1	5	0	0	1	1*	0	1	0	0	×	0	2+	0
(snails)		3	55	×	×	×	4	1	25	12	5	3	4	0	1	0	0	0	×	30	40	1
		1	6	0	1	1	2	0	0	1	0	0	0	0	0	0	1	0	1—	1—	1—	0
Isopoda	7	2	1	×	×	×	0	0	0	0	0	0	1	0	0	0	0	0	×	0	1—	0
(sow-bugs)		3	0	×	×	×	0	0	0	0	0	0	0	0	0	0	0	0	×	0	0	0
		1	9	0	1	1	0	1	0	0	0	2	1	0	0	0	3	0	1—	1—	1	0
Myriapoda (centipedes and	73	2	39	×	×	×	2	4	0	1	1	0	1	3*	6	8	9	4	×	2—	5—	4
millipedes)		3	25	×	×	×	1	0	0	0	0	2	0	3	1	0	7	11	×	1—	2+	11
		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chelonethida (pseudo-	4	2	1	×	×	×	0	0	0	1	0	0	0	0	0	0	0	0	×	1—	0	0
scorpions)		3	3	×	×	×	0	0	1	0	0	0	1	0	1	0	0	0	×	1—	1—	0
		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Phalangida	401	2	14	×	×	×	0	0	0	0	0	0	0	13*	1	0	0	0	×	0	2+	0
(harvestmen)		3	387	×	×	×	0	17	12	99	21	2	7	198	27	3	0	1	×	30	40	1
		1	403	15	34	14	8	18	19	31	27	14	69	24*	39	43	27	21	21	21	36	21
Araneida	846	2	250	×	×	×	25	22	22	26	31	9	7	11*	28	23	26	20	×	25	17	20
(spiders)		3	193	×	×	×	34	14	7	25	14	12	13	22	13	12	14	13	×	19	14	13

TABLE 26.—(*Continued*)

Population breakdown	No. of specimens collected	Station	Station totals	Total numbers for two-week period ending: 1939 Apr 22	May 6	May 20	Jun. 3	Jun. 17	Jul. 1	Jul. 15	Aug. 29	Aug. 12	Aug. 26	Sep. 9	Sep. 23	Oct. 7	Oct. 21	Nov. 4	Seasonal average per unit collection: Vernal	Estival	Autumnal	Hiemal
Orthoptera		1	312	1	14	14	21	41	39	32	15	30	20	27*	24	17	6	11	10	30	21	11
(grasshoppers,	821	2	222	×	×	×	24	18	22	14	16	10	11	23*	31	30	14	9	×	19	20	9
etc.)		3	287	×	×	×	11	19	42	88	29	7	3	25	24	22	13	4	×	38	16	4
		1	31	1	2	4	2	3	1	1	1	0	2	2*	6	3	2	1	2+	2—	3—	1
Hemiptera	1,552	2	57	×	×	×	2	0	0	0	1	1	2	0	3	17	25	6	×	1—	8	6
(true bugs)		3	1,464	×	×	×	28	14	9	3	5	39	200	963	166	21	12	4	×	12	234	4
		1	1,085	40	76	59	132	298	132	116	45	45	17	23*	47	37	15	3	58	145	31	3
Coleoptera	2,906	2	718	×	×	×	103	145	77	62	43	20	23	39*	60	93	30	23	×	86	44	23
(beetles)		3	1,103	×	×	×	51	72	67	82	87	191	135	128	125	87	59	19	×	72	121	19
Hymenoptera		1	1,989	3	25	27	56	76	220	450	283	212	99	158*	154	144	47	35	18	217	136	35
(ants and	3,266	2	888	×	×	×	50	62	95	66	53	36	37	71*	68	229	73	48	×	65	88	48
velvet ants		3	389	×	×	×	11	20	32	15	7	8	5	12	52	100	89	38	×	17	44	38
		1	896	4	8	4	7	4	21	143	53	136	188	265*	49	13	1	0	5	46	130	0
Larvae	1,221	2	208	×	×	×	12	4	20	19	12	30	27	48*	15	12	6	3	×	13	23	3
		3	117	×	×	×	12	12	37	13	3	8	12	6	7	4	3	0	×	15	7	0
Total		1	4,731	64	161	124	228	441	432	774	424	439	396	499	319	257	102	71	116	460	335	71
population	11,161	2	2,407	×	×	×	218	255	237	194	157	106	110	209	212	413	183	113	×	212	206	113
(as studied)		3	4,023	×	×	×	152	169	232	337	171	272	380	1357	417	249	197	90	×	212	479	90

* Collection for second week lost; two-week total derived by interpolating for the second week the average of the preceding and following week. × No collection.

TABLE 27.—Annotated list of prevalents.

Class	Order	Family	Prevalent	Station	Attained prevalence in Stratum	Season
Annelida	Oligochaeta (Class)	Enchytraeidae	Fridericia spp.	True prairie subsere, shrub	Litter	Prevernal-vernal, estival
				Tall grass	Litter	Estival
Arachnida	Phalangida	Phalangidae	Leiobunum sp.	Shrub	Ground surface	Estival
Insecta	Orthoptera	Acrididae	Melanoplus bivittatus (Say)	Tall grass	Herb	Prevernal-vernal
	Hemiptera	Miridae	Lygus pratensis (Linnaeus)	Tall grass	Herb	Autumnal
		Lygaeidae	Blissus leucopterus (Say)	Tall grass	Litter	Prevernal-vernal, hiemal
		Cydnidae	Geotomus robustus (Uhler)	Shrub	Soil & ground surface	Autumnal
		Tingidae	Piesma cinerea Say	True prairie subsere, tall grass	Litter	Hiemal
	Homoptera	Cicadellidae	Balclutha abdominalis (V.D.)	True prairie subsere	Herb	Prevernal-vernal, estival and autumnal
				Tall grass	Herb	Estival
				Shrub	Herb	Prevernal-vernal
			Dikraneura abnormis (Walsh)	Shrub	Herb	Autumnal
			Erythroneura sp.	Shrub	Shrub	Estival-autumnal
		Fulgoridae	Delphacodes sp.	True prairie subsere	Herb	Hiemal
		Aphidae	Anoecia graminis Gillette & Palmer	Shrub	Herb	Early hiemal
	Coleoptera	Carabidae	Amara sp.	True prairie subsere	Soil	Annual
					Litter	Autumnal
					Ground surface	Prevernal-vernal
				Tall grass	Soil	Annual
		Scarabaeidae	Ataenius cognatus Lec.	Shrub	Soil	Early hiemal
		Chrysomelidae	Chalcoides fulvicornis (Fabr.)	Shrub	Shrub	Prevernal-vernal
	Hymenoptera	Formicidae	Crematogaster lineolata Say	True prairie subsere	Ground surface	Autumnal, early hiemal
				Tall grass	Ground surface	Estival
			Prenolepis imparis Say	Tall grass and shrub	Ground surface	Early hiemal
			Dorymyrmex pyramicus Roger	True prairie subsere	Ground surface	Estival

TABLE 28.—Annotated list of subprevalents.

Class	Order	Family	Subprevalent	Attained subprevalence in		
				Station	Stratum	Season
Mollusca	Pulmonata	Pupillidae	Gastrocopta armifera (Say)	Shrub	Litter	Estival
Insecta	Orthoptera	Gryllidae	Oecanthus niveus (DeG.)	True prairie subsere	Herb	Autumnal
	Hemiptera	Pentatomidae	Thyanta custator (Fabr.)	Tall grass	Herb	Late autumnal
				Shrub	Herb	Late autumnal
		Anthocoridae	Orius insidiosus Say	Shrub	Litter	Hiemal
	Homoptera	Cicadellidae	Macrosteles divisus (Uhl.)	Tall grass	Herb	Estival
		Cicadellidae	Empoasca sp.	Shrub	Herb	Late autumnal
		Psyllidae	Aphalara veaziei Patch	True prairie subsere	Herb	Early estival
	Coleoptera	Chrysomelidae	Pachybrachys litigiosus Suffr.	True prairie subsere	Herb	Early estival
		Tenebrionidae	Eleodes opaca Say	True prairie subsere	Ground surface	Estival
		Coccinellidae	Hippodamia convergens Guer.	Tall grass	Litter	Hiemal
		Carabidae	Agonoderus pallipes Fabr.	Tall grass	Ground surface	Autumnal
		Staphylinidae	Oxypoda sp.	Shrub	Litter	Hiemal
	Diptera	Chloropidae	Madiza sp.	Shrub	Herb	Vernal
		Chloropidae	Oscinella coxendix (Fitch)	Shrub	Herb	Late autumnal
		Chloropidae	Oscinella minor Adams	True prairie subsere	Herb	Autumnal
		Empididae	Rhamphomyia sp.	Shrub	Herb	Estival
		Empididae	Tachydromia maculipennis Walker	Shrub	Shrub	Prevernal-vernal
	Hymenoptera	Formicidae	Aphaenogaster fulva aquia Buckley	True prairie subsere	Herb	Autumnal
			Tapinoma sessile Say	True prairie subsere	Herb	Autumnal
			Pheidole bicarinata Mays	True prairie subsere	Herb	Autumnal
			Leptothorax curvispinosus ambiguus Emery	Shrub	Litter	Hiemal
			Ponera coarctata pennsylvanicus Buckley	True prairie subsere	Litter	Prevernal-vernal, early estival

TABLE 29.—Spatial and chronological distribution of prevalents of true prairie subsere throughout the periods, stations, and strata in which these animals were collected.

Average number per unit collection for two-week period ending

Prevalent	Stratum	Station	1937 Nov. 16	17	1938 Jan. 14	Feb. 28	Mar. 11	Apr. 25	9	May 23	6	Jun. 20	4	Jul. 18	1	Aug. 15	29	Sep. 12	24*	Oct. 8	22	Nov. 5	19	1939 Dec. 3	17	Jan. 14	28	Feb. 11	Mar. 25	Seasonal averages per unit collection: Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal
Balclutha abdominalis	Herb	Prairie subsere	0	x	x	0	0	0	12	13	72	235	133	43	25	4	2+	27	67	113	46	1—0		0	x	0	x	0	0	0	6	93	23	1—
		Tall grass	0	x	x	0	0	0	8	71	48	29	10	10	11	14	8	2	0	4	3	1—0		0	x	0	x	0	0	0	20	17	6	1—
		Shrub	0	x	x	1	0	3	—43	34	30	33	77	14	1—	0	0	0	0	0	0	0	1	0	x	0	x	0	0	1—	20	43	0	1—
Delphacodes sp.	Herb	Prairie subsere	0	x	x	0	0	0	0	0	3	2+	10	47	48	3—	6	8	13	0	10	5	5	2—x		1	x	1	4	0	0	25	7	3+
		Tall grass	0	x	x	0	0	0	1	1—	0	2—	9	29	55	27	8	8	0	12	3+	1+	1	1—x		1—x		0	1—	0	1—18		12	1—
Crematogaster lineolata	Herb	Prairie subsere	0	x	x	0	0	0	1	0	5—	6	2+	2—	5	1+	1—	1+	1	0	0	0	0	0	x	0	x	0	0	0	1—	4—	1—0	
		Tall grass	0	x	x	0	0	0	11	15	20	9	6	1	1—	1	0	1	2	0	0	0	0	0	x	0	x	0	0	0	6	6	1—0	
		Shrub	0	x	x	1—0		3	20	18	11	8	15	11	4—	5—	7	x	1	1	1—0		0	0	x	0	x	0	0	1—	8	11	3—0	
	Shrub	Shrub	x	x	x	x	x	23	25	30	30	0	2	0	0	5	35	0	0	x	x	x	x	x	x	x	x	x	x	x	26	5	13	x
	Litter	Prairie subsere	x	0	x	2	0	1—	1	7	1	1	1	2	2	0	0	x	x	x	0	0	0	0	0	0	0	0	0	2—	1	2	1+	0	1—
		Tall grass	x	0	0	0	0	2	9	1—25		x	0	1	1	x	x	x	x	x	1—0		0	0	0	0	0	0	0	0	1	5—	1—0	
		Shrub	x	0	0	0	0	0	0	0	6	x	2—	0	0	0	x	x	x	x	0	0	0	0	0	0	0	0	0	0	0	2—	0	0

Total numbers for two-week periods ending

Prevalent	Stratum	Station	1939 Apr. 22	6	May 20	3	Jun. 17	1	Jul. 15	29	12	Aug. 26	9	Sep. 23	7	Oct. 21	Nov. 4	Seasonal averages per unit collection period (two weeks): Vernal Estival	Autumnal	Early Hiemal
Crematogaster lineolata	Ground surface	Prairie subsere	7	6	4	27	32	59	71	207	100	57	97	102	51	31	17	6	79	73	17
		Tall grass	x	x	x	24	31	42	28	36	14	13	18	14	33	12	5	x	32	17	5
		Shrub	x	x	x	4	9	11	9	4	6	2	5	12	4	9	2	x	7	6	2
Dorymyrmex pyramicus	Ground surface	Prairie subsere	0	0	0	0	6	64	293	6	6	2	0	0	0	0	0	0	74	1+	0
Amara sp.	Ground surface	Prairie subsere	0	18	14	27	70	12	2	0	1—	0	0	0	0	0	0	16	22	1—	0
		Tall grass	x	x	x	4	6	1	0	0	0	0	0	0	0	0	0	x	2+	0	0
		Shrub	x	x	x	1—	2—	1—	0	0	0	0	0	0	0	0	0	x	1—	0	0

* Short period. x No collection.

TABLE 30.—Spatial and chronological distribution of prevalents of postclimax tall grass throughout the periods, stations, and strata in which these animals were collected.

Prevalent	Stratum	Station	Average number per unit collection for two-week periods ending																												Seasonal averages per unit collection				
			1937		1938																				1939										
			Nov.		Jan.		Feb.	Mar.		Apr.		May		Jun.		Jul.			Aug.		Sep.		Oct.		Nov.		Dec.		Jan.		Feb.	Mar.	Hiemal	Prevernal vernal	Estival	Autumnal	Hiemal
			16	17	14	28	11	25	9	23	6	20	4	18	1	15	29	12	24*	8	22	5	19	3	17	14	28	11	25						
Melanoplus bivittatus	Herb	Prairie subsere	0	x	x	0	0	0	5	6	17	11	8	8	5	1	1	0	0	0	0	0	0	0	x	0	x	0	0	0	3	9	1	0
		Tall grass	0	x	x	0	0	0	8	67	46	23	16	15	6	11	3	1	1	0	1	0	0	0	x	0	x	0	0	0	19	18	4	0
		Shrub	0	x	x	0	0	0	14	30	19	10	4	5	2	3	2	x	1	1	0	0	0	0	x	0	x	0	0	0	11	7	1	0
	Shrub	Shrub	x	x	x	x	x	0	0	0	0	0	2	5	0	10	0	x	0	x	x	x	x	x	x	x	x	x	0	x	0	2	3	x
Lygus pratensis	Herb	Prairie subsere	1	x	x	0	0	0	0	0	0	6	3	1	0	0	0	0	1	0	0	0	0	0	x	0	x	0	1	1	0	2	1	1
		Tall grass	14	x	x	5	0	0	0	0	0	0	1	1	1	0	0	0	1	7	80	6	1	0	x	0	x	0	6	11	0	1	23	2
		Shrub	27	x	x	20	1	1	3	†	†	0	0	0	●	0	0	x	0	11	19	27	12	1	x	0	x	0	2	24	1	0	6	7
	Litter	Tall grass	x	0	0	0	0	0	0	0	0	x	0	0	0	x	x	x	x	x	0	6	0	0	0	0	0	0	0	0	0	0	2	0
		Shrub	x	3	1	0	1	0	0	0	0	x	0	0	0	0	x	x	x	x	0	1	0	5	4	5	0	2	1	1	1	0	1	2
Blissus leucopterus	Herb	Prairie subsere	0	x	x	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	x	0	x	0	0	0	0	0	0	1	0
		Tall grass	0	x	x	0	0	0	5	0	4	0	0	0	0	0	0	0	0	1	9	1	0	0	x	0	x	0	1	0	1	3	1	0
		Shrub	0	x	x	1	0	0	2	0	0	0	0	0	0	0	1	x	1	0	0	0	0	x	0	x	0	0	1	0	1	3	1	0
	Litter	Prairie subsere	x	0	x	1	0	0	0	0	0	0	0	0	0	0	0	x	x	x	0	0	0	0	0	0	0	0	0	1	0	0	0	0
		Tall grass	x	0	0	0	16	9	1	0	0	x	0	0	0	x	x	x	x	x	1	1	3	51	1	0	18	14	1	0	11	1	1	14
		Shrub	x	1	2	3	1	1	0	0	0	x	0	0	0	0	x	x	x	x	3	3	3	0	17	1	1	2	1	2	1	0	2	4
Piesma cinerea	Herb	Prairie subsere	0	x	x	0	0	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	x	0	x	0	0	0	1	1	1	0
		Tall grass	0	x	x	0	0	0	34	4	0	0	0	0	0	0	0	1	0	1	0	0	0	0	x	0	x	0	0	0	9	1	1	0
		Shrub	0	x	x	0	0	0	1	7	3	4	1	0	0	0	0	1	1	2	11	3	3	1	0	x	0	x	0	0	3	1	2	1
	Shrub	Shrub	x	x	x	x	x	0	3	5	3	0	1	0	0	0	5	x	0	x	x	x	x	x	x	x	x	x	0	x	3	1	2	x
	Litter	Prairie subsere	x	1	x	0	0	0	0	0	0	0	0	0	0	0	0	x	x	x	0	1	2	6	0	1	0	2	0	1	0	0	1	1
		Tall grass	x	0	0	1	1	0	1	0	0	x	0	0	0	x	x	x	x	4	1	6	18	10	0	24	5	6	1	1	1	3	10
		Shrub	x	3	0	1	1	1	1	1	1	6	x	0	0	0	x	x	x	x	3	5	8	5	12	18	8	34	4	1	1	0	3	13
Fridericia sp.	Litter	Prairie subsere	x	0	x	0	0	2	1	0	0	11	7	0	0	0	0	x	x	x	0	0	2	0	0	0	0	0	0	0	3	4	0	1
		Tall grass	x	0	0	9	6	11	21	18	1	x	47	0	0	x	x	x	x	0	0	5	0	1	0	0	2	1	4	8	19	0	1
		Shrub	x	0	0	25	75	117	20	15	0	x	13	2	0	0	x	x	x	x	0	0	77	40	2	0	0	0	0	13	62	4	0	9
Amara sp.	Litter	Prairie subsere	x	0	x	1	0	0	3	5	0	0	1	0	1	0	0	x	x	x	x	5	0	0	0	0	0	0	0	11	1	2	1	2	1
		Tall grass	x	0	0	0	0	4	1	6	0	x	2	1	0	x	x	x	x	x	0	0	0	0	0	0	0	1	0	0	2	2	0	1
	Soil	Prairie subsere	x	x	x	x	1	0	0	3	4	0	0	0	1	x	x	x	x	0	12	6	0	5	1	x	0	1	x	x	1	1	4	2
		Tall grass	x	x	x	x	0	16	3	2	0	x	3	2	0	x	x	x	x	0	1	0	1	10	1	x	9	1	x	x	5	1	1	4

* Short period. † Many nymphs. x No collection.

TABLE 31.—Spatial and chronological distribution of the prevalents of postclimax deciduous shrub throughout the periods, stations, and strata in which these animals were collected.

Average number per unit collection for two-week periods ending

Prevalent	Stratum	Station	1937 Nov. 16	17	1938 Jan. 14	Feb. 28	Mar. 11	Apr. 25	May 9	23	Jun. 6	20	Jul. 4	18	Aug. 1	15	29	Sep. 12	24*	Oct. 8	22	Nov. 5	19	Dec. 3	17	Jan. 14	28	Feb. 11	Mar. 25	Hiemal	Prevernal-vernal	Estival	Autumnal	Hiemal
Chalcoides fulvicornis	Shrub	Shrub	x	x	x	x	x	183	167	68	58	45	13	8	0	0	35	x	0	x	x	x	x	x	x	x	x	0	x	104	18	12	x
	Herb	Shrub	0	x	x	0	0	5—	2—	1—	2—	1—	0	0	0	0	0	x	0	0	0	0	0	0	x	0	x	0	0	0	2—	1—	0	0
Erythroneura sp.	Shrub	Shrub	x	x	x	x	x	10	10	13	25	5	32	103	175	145	160	x	0	x	x	x	x	x	x	x	x	x	0	x	11	65	102	x
Dikraneura abnormis	Herb	Shrub	0	x	x	0	0	0	0	0	0	0	8	28	122	108	209	x	15	123	102	3	3—	0	x	0	x	0	0	0	0	27	98	1—
Anoecia graminis	Herb	Shrub	1—	x	x	0	0	0	1—	2—	7	3—	8	9	0	0	0	x	2	51	297	129	21	4—	x	1—	x	3	0	1—	1—	5—	81	24
Prenolepis imparis	Herb	Tall grass	1—	x	x	0	0	0	1—	9	4—	7	2—	1—	0	0	0	0	0	0	0	0	1—	0	x	0	x	0	0	0	6	6	1—	0
		Shrub	4—	x	x	0	1—	6	30	29	13	19	4—	3	0	1	0	x	7	70	120	48	14	0	x	0	x	0	0	3—	16	8	41	9
	Shrub	Shrub	x	x	x	x	x	23	25	30	0	0	3—	0	0	0	35	x	0	x	x	x	x	x	x	x	x	x	0	x	24	8	0	x
Leiobunum sp.	Herb	Shrub	0	x	x	0	0	0	0	0	0	1—	1—	1	1	0	1	x	1—	0	0	0	0	0	0	x	0	x	0	0	0	1—	1—	0
Ataenius cognatus	Litter	Shrub	x	0	0	2—	0	2—	0	0	0	x	0	0	1—	0	x	x	x	x	0	0	0	0	0	0	0	0	0	1—	1—	1—	0	0
	Soil	Shrub	x	x	x	x	0	0	0	0	0	x	0	0	0	x	6	x	x	2	4	3	6	11	6	x	6	1	x	x	0	0	4—	5

Total numbers for two-week periods ending

Prevalent	Stratum	Station	1939 Apr. 22	May 6	20	Jun. 3	17	Jul. 1	15	29	Aug. 12	26	Sep. 9	23	Oct. 7	21	Nov. 4	Vernal	Estival	Autumnal	Early Hiemal
Prenolepis imparis	Ground surface	Prairie subsere	0	0	0	1	11	2	42	21	37	14	0	18	19	9	4	0	15	16	4
		Tall grass	x	x	x	0	9	4	11	0	0	1	0	22	22	29	26	x	5	12	26
		Shrub	x	x	x	0	5	0	0	0	0	0	1	33	76	72	36	x	1	30	36
Leiobunum sp.	Ground surface	Tall grass	0	0	0	0	0	0	0	0	0	0	13	1	0	0	0	0	0	2	0
		Shrub	x	x	x	0	17	12	99	21	2	7	198	27	3	0	1	x	30	40	1
Geotomus robustus	Ground surface	Shrub	x	x	x	24	12	7	1	2	22	181	940	159	7	2	0	x	9	219	0
Ataenius cognatus	Ground surface	Shrub	x	x	x	11	4	0	11	30	163	108	36	5	16	21	1	x	11	58	1

Seasonal averages per unit collection

Seasonal averages per unit collection period (two weeks)

* Short period. x No collection.

TABLE 32.—Actual unit collection numbers of invertebrates taken by sweep net method of sampling invertebrate populations (169 unit collections; 117 day, 52 night) in the herb stratum of true prairie subsere (Station 1) and postclimax tall grass (Station 2), and in the herb and shrub strata of postclimax deciduous shrub (Station 3), during delimited periods comprising forenoon, afternoon, early night, and late night. Based on 57,277 specimens taken from June 12 to October 29, 1938, the first week of the hiemal aspect, as defined in this study, being included in the autumnal here.

	Date	Station 1 Herb				Station 2 Herb				Station 3 Herb				Station 3 Shrub*			
		8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.
ESTIVAL.	1938, Jun. 12	—	563	—	—	—	304	—	—	—	532	—	—	—	800	—	—
	17	798	907	—	—	180	291	—	—	502	334	—	—	470	520	—	—
	18	—	—	944	—	—	—	215	—	—	—	472	—	—	—	680	—
	19	—	—	—	496	—	—	—	—	—	—	—	—	—	—	—	—
	21	—	653	—	—	—	231	—	—	—	657	—	—	—	615	—	—
	23	614	452	650	—	237	204	196	—	530	—	—	—	285	—	—	—
	25	296	—	—	—	135	—	—	—	146	—	—	—	—	—	—	—
	28	440	—	—	—	188	—	—	—	355	—	—	—	635	—	—	—
	29	—	—	159	—	—	—	109	—	—	—	—	—	—	—	—	—
	30	—	231	—	140	—	—	—	114	—	—	—	—	—	—	—	—
	30	—	—	—	169	—	—	—	—	—	—	—	—	—	—	—	—
	Jul. 1	309	522	—	—	201	463	—	—	499	326	—	—	695	555	—	—
	2	—	466	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	5	—	374	—	—	—	198	—	—	—	—	—	—	—	—	—	—
	7	—	384	393	—	—	162	324	—	—	333	—	—	—	525	—	—
	8	399	—	—	—	197	—	—	—	—	—	—	—	—	—	—	—
	9	259	462	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	15	—	—	—	—	—	445	—	—	—	859	—	—	—	720	—	—
	18	—	—	457	—	—	—	543	—	—	—	—	—	—	—	—	—
	19	—	—	—	346	—	—	—	429	—	—	—	—	—	—	—	—
	21	—	—	381	—	—	—	237	—	—	—	264	—	—	—	290	—
	22	359	317	—	—	—	386	—	—	—	613	—	—	—	425	—	—
	26	—	583	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	28	—	386	705	—	—	340	443	—	—	577	—	—	—	1125	—	—
	29	462	—	—	—	293	—	—	—	—	—	—	—	—	—	—	—
	Aug. 1	—	245	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	2	117	—	—	—	—	—	—	—	495	—	—	—	—	—	—	—
	3	—	—	409	—	—	—	489	—	—	—	495	—	—	—	470	—
	4	—	—	427	—	—	—	413	—	—	—	—	—	—	—	—	—
	5	175	323	—	—	246	317	—	—	—	495	—	—	—	465	—	—
	6	—	—	—	231	—	—	—	213	—	—	—	530	—	—	—	355
	6	—	—	—	261	—	—	—	181	—	—	—	—	—	—	—	—
	10	—	—	324	—	—	—	351	—	—	—	—	—	—	—	—	—
	10	—	—	238	—	—	—	346	—	—	—	—	—	—	—	—	—
	11	—	—	—	380	—	—	—	166	—	—	—	259	—	—	—	510
	12	—	193	—	—	—	257	—	—	—	—	—	—	—	—	—	—

* Actual collection numbers multiplied by 5.

TABLE 32.—(*Continued*)

AUTUMNAL		12	—	214	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	258	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		15	—	485	—	—	—	353	—	—	—	—	—	—	—	—	—	—	—
		22	—	55	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		22	—	233	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		22	—	78	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		25	—	72	—	—	—	—	—	—	—	635	—	—	—	490	—	—	—
		25	—	199	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		25	—	101	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		29	207	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Sep.	3	—	—	241	—	—	—	214	—	—	—	—	—	—	—	—	—	—
		5	—	250	—	—	—	259	—	—	—	—	—	—	—	—	—	—	—
		5	—	183	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		7	159	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		9	—	—	—	—	95	—	—	—	—	—	—	—	—	—	—	—	—
		12	603	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		18	—	187	—	—	—	132	—	—	—	—	—	—	—	0	—	—	—
		18	—	178	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Oct.	1	217	—	—	—	225	—	—	—	1202	—	—	—	—	—	—	—	—
		7	—	—	438	—	—	—	510	—	—	—	925	—	—	—	—	—	—
		8	234	—	—	—	258	—	—	—	2614	—	—	—	—	—	—	—	—
		15	106	—	—	—	156	—	—	—	2149	—	—	—	—	—	—	—	—
		15	—	—	—	—	382	—	—	—	—	—	—	—	—	—	—	—	—
		18	—	—	—	—	—	—	—	—	—	206	—	—	—	—	—	—	—
		18	—	—	—	—	—	—	—	—	—	148	—	—	—	—	—	—	—
		21	—	—	25	—	—	—	101	—	—	—	965	—	—	—	—	—	—
	Early hiemal	22	3	—	—	—	6	—	—	—	316	—	—	—	—	—	—	—	—
		29	30	—	—	—	41	—	—	—	697	—	—	—	—	—	—	—	—
		29	—	—	—	—	85	—	—	—	—	—	—	—	—	—	—	—	—
Total number of specimens	Estival		3936	6300	3689	1151	1431	3024	2067	543	2032	4231	736	—	2085	5285	970	—	
	Autumnal		1851	3254	2102	872	1494	1318	2424	560	7473	1484	2385	789	—	955	470	865	
	Jun. 12-Oct. 29		5787	9554	5791	2023	2925	4342	4491	1103	9505	5715	3121	789	2085	6240	1440	865	
Total number of collections	Estival		9	13	7	4	7	10	7	2	5	8	2	0	4	8	2	0	
	Autumnal		10	16	7	3	9	5	7	3	6	4	3	2	0	3	1	2	
	Jun. 12-Oct. 29		19	29	14	7	16	15	14	5	11	12	5	2	4	11	3	2	
Average number of specimens per collection	Estival		437	485	527	288	204	302	295	272	406	529	368	—	521	661	485	—	
	Autumnal		185	203	300	291	166	264	346	187	1246	371	795	395	—	318	470	433	
	Jun. 12-Oct. 29		305	329	414	289	183	289	321	221	864	476	624	395	521	567	480	433	

* Actual collection numbers multiplied by 5.

TABLE 33.—Average numbers of prevalents per unit collection taken by sweep net method of sampling invertebrate populations (169 unit collections; 117 day, 52

TABLE 33.—Average numbers of prevalents per unit collection taken by sweep net method of sampling invertebrate populations (169 unit collections; 117 day, 52 night) in the herb stratum of true prairie subsere (Station 1) and postclimax tall grass (Station 2), and in the herb and shrub strata of postclimax deciduous shrub (Station 3), during delimited periods comprising forenoon, afternoon, early night, and late night. Averages are seasonal and for the entire period of the day-night studies, June 12 to October 29, 1938, the first week of the hiemal aspect, as defined in this study, being included in the autumnal here.

Prevalent		Station 1 Herb				Station 2 Herb				Station 3 Herb				Station 3 Shrub			
		8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.
Chalcoides fulvicornis	Estival	0	0	0	0	0	0	0	0	0	1—	1—	—	20	17	15	—
	Autumnal	0	0	0	0	0	0	0	0	0	0	0	0	—	12	0	10
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	0	1—	1—	0	20	15	10	10
Erythroneura sp.	Estival	0	0	0	0	0	0	0	0	0	0	0	—	35	74	23	—
	Autumnal	0	0	0	0	0	0	0	0	0	0	0	0	—	101	135	163
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	0	0	0	0	35	81	60	163
Balclutha abdominalis	Estival	86	101	87	27	8	18	6	4	60	37	48	—	0	0	0	—
	Autumnal	42	9	22	2+	4	6	8	4	0	0	0	0	—	0	0	0
	Jun. 12-Oct. 29	63	50	55	17	6	14	7	4	27	24	19	0	0	0	0	0
Delphacodes sp.	Estival	26	26	21	5	20	21	39	15	0	0	0	—	0	0	0	—
	Autumnal	10	5	14	21	9	15	66	24	0	0	0	0	—	0	0	0
	Jun. 12-Oct. 29	19	14	17	12	15	19	52	20	0	0	0	0	0	0	0	0
Melanoplus bivittatus	Estival	7	9	6	5—	14	16	19	11	5	5	8	—	3—	1+	13	—
	Autumnal	1—	1—	3—	3	1+	6	11	15	1—	2	1—	4—	—	3+	0	8
	Jun. 12-Oct. 29	4—	4+	4+	4—	7	11	15	13	3—	4	3+	4—	3—	2—	8	8
Lygus pratensis	Estival	1—	3+	1—	4—	1—	1—	1—	4	0	0	0	—	0	0	0	—
	Autumnal	0	1—	1—	0	30	1—	1—	0	17	0	9	0	—	0	0	0
	Jun. 12-Oct. 29	1—	2—	1—	2+	17	1—	1—	2—	9—	0	6	0	0	0	0	0
Dikraneura abnormis	Estival	0	0	0	0	0	0	0	0	6	40	18	—	0	0	0	—
	Autumnal	0	0	0	0	0	0	0	0	76	83	66	101	—	0	0	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	44	54	47	101	0	0	0	0
Anoecia graminis	Estival	0	0	0	0	0	0	0	0	11	0	3—	—	0	0	0	—
	Autumnal	0	0	0	0	0	0	0	0	161	1	35	0	—	0	0	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	78	1—	22	0	0	0	0	0
Crematogaster lineolata	Estival	4—	3+	3+	1+	2	7	1—	1—	13	9	13	—	3—	0	0	—
	Autumnal	1—	1—	4—	1	1—	1	3	3—	1—	4—	2—	17	—	13	55	28
	Jun. 12-Oct. 29	2—	2	3+	1+	1+	5—	2—	2—	8	7	6	17	3—	4—	18	28
Prenolepis imparis	Estival	0	1—	0	0	1	3+	3+	1	7	6	20	—	3—	3+	0	—
	Autumnal	1—	0	0	0	0	0	1—	4—	78	4—	32	3	—	0	0	3—
	Jun. 12-Oct. 29	1—	1—	0	0	1—	2+	2+	3—	39	5	27	3	3—	2+	0	3—
Leiobunum sp.	Estival	0	0	0	0	0	0	1—	0	1—	1—	2	—	0	0	0	—
	Autumnal	0	0	0	0	0	0	0	1—	0	1—	0	1	—	0	1	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	1—	1—	1—	1—	1—	1	0	0	1—	0
Blissus leoucopterus	Estival	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—
	Autumnal	1—	1—	0	0	3+	0	1—	0	0	1—	0	0	—	0	0	0
	Jun. 12-Oct. 29	1—	1—	0	0	2—	0	1—	0	0	1—	0	0	0	0	0	0
Piesma cinerea	Estival	1—	1—	0	0	0	0	0	0	0	1—	1—	0	0	1—	0	—
	Autumnal	1—	1—	0	0	1—	1—	0	0	4—	2—	3	0	—	2+	0	0
	Jun. 12-Oct. 29	1—	1—	0	0	1—	1—	0	0	2	1—	2	0	0	1—	0	0

TABLE 32.—(*Continued*)

AUTUMNAL		12	—	214	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		12	—	258	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		15	—	485	—	—	—	333	—	—	—	—	—	—	—	—	—	—	—
		22	—	55	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		22	—	233	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		22	—	78	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		25	—	72	—	—	—	—	—	—	—	635	—	—	—	490	—	—	—
		25	—	199	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		25	—	101	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		29	207	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Sep.	3	—	—	241	—	—	—	214	—	—	—	—	—	—	—	—	—	—
		5	—	250	—	—	—	259	—	—	—	—	—	—	—	—	—	—	—
		5	—	183	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		7	159	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		9	—	—	—	—	95	—	—	—	—	—	—	—	—	—	—	—	—
		12	603	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
		18	—	187	—	—	—	132	—	—	—	—	—	—	—	0	—	—	—
		18	—	178	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	Oct.	1	217	—	—	—	225	—	—	—	1202	—	—	—	—	—	—	—	—
		7	—	—	438	—	—	—	510	—	—	—	923	—	—	—	—	—	—
		8	234	—	—	—	258	—	—	—	2614	—	—	—	—	—	—	—	—
		15	106	—	—	—	156	—	—	—	2149	—	—	—	—	—	—	—	—
		15	—	—	—	—	382	—	—	—	—	—	—	—	—	—	—	—	—
		18	—	—	—	—	—	—	—	—	—	206	—	—	—	—	—	—	—
		18	—	—	—	—	—	—	—	—	—	148	—	—	—	—	—	—	—
		21	—	—	25	—	—	—	101	—	—	—	965	—	—	—	—	—	—
	Early hiemal	22	3	—	—	—	6	—	—	—	316	—	—	—	—	—	—	—	—
		29	30	—	—	—	41	—	—	—	697	—	—	—	—	—	—	—	—
		29	—	—	—	—	85	—	—	—	—	—	—	—	—	—	—	—	—
Total number of specimens	Estival		3936	6300	3689	1151	1431	3024	2067	543	2032	4231	736	—	2085	5285	970	—
	Autumnal		1851	3254	2102	872	1494	1318	2424	560	7473	1484	2385	789	—	955	470	865
	Jun. 12-Oct.	29	5787	9554	5791	2023	2925	4342	4491	1103	9505	5715	3121	789	2085	6240	1440	865
Total number of collections	Estival		9	13	7	4	7	10	7	2	5	8	2	0	4	8	2	0
	Autumnal		10	16	7	3	9	5	7	3	6	4	3	2	0	3	1	2
	Jun. 12-Oct.	29	19	29	14	7	16	15	14	5	11	12	5	2	4	11	3	2
Average number of specimens per collection	Estival		437	485	527	288	204	302	295	272	406	529	368	—	521	661	485	—
	Autumnal		185	203	300	291	166	264	346	187	1246	371	795	395	—	318	470	433
	Jun. 12-Oct.	29	305	329	414	289	183	289	321	221	864	476	624	395	521	567	480	433

* Actual collection numbers multiplied by 5.

TABLE 33.—Average numbers of prevalents per unit collection taken by sweep net method of sampling invertebrate populations (169 unit collections; 117 day, 52 night) in the herb stratum of true prairie subsere (Station 1) and postclimax tall gram (Station 2), and in the herb and shrub strata of postclimax deciduous shrub (Station 3), during delimited periods comprising forenoon, afternoon, early night, and late night. Averages are seasonal and for the entire period of the day-night studies, June 12 to October 29, 1938, the first week of the hiemal aspect, as defined in this study, being included in the autumnal here.

Prevalent		Station 1 Herb				Station 2 Herb				Station 3 Herb				Station 3 Shrub			
		8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.	8-11 A.M.	2-6 P.M.	9-11 P.M.	1-4 A.M.
Chalcoides fulvicornis	Estival	0	0	0	0	0	0	0	0	0	1—	1—	—	20	17	15	—
	Autumnal	0	0	0	0	0	0	0	0	0	0	0	0	—	12	0	10
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	0	1—	1—	0	20	15	10	10
Erythroneura sp.	Estival	0	0	0	0	0	0	0	0	0	0	0	—	35	74	23	—
	Autumnal	0	0	0	0	0	0	0	0	0	0	0	0	—	101	135	163
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	0	0	0	0	35	81	60	163
Balclutha abdominalis	Estival	86	101	87	27	8	18	6	4	60	37	48	—	0	0	0	—
	Autumnal	42	9	22	2+	4	6	8	4	0	0	0	0	—	0	0	0
	Jun. 12-Oct. 29	63	50	55	17	6	14	7	4	27	24	19	0	0	0	0	0
Delphacodes sp.	Estival	26	26	21	5	20	21	39	15	0	0	0	—	0	0	0	—
	Autumnal	10	5	14	21	9	15	66	24	0	0	0	0	—	0	0	0
	Jun. 12-Oct. 29	19	14	17	12	15	19	52	20	0	0	0	0	0	0	0	0
Melanoplus bivittatus	Estival	7	9	6	5—	14	16	19	11	5	5	8	—	3—	1+	13	—
	Autumnal	1—	1—	3—	3	1+	6	11	15	1—	2	1—	4—	—	3+	0	8
	Jun. 12-Oct. 29	4—	4+	4+	4—	7	11	15	13	3—	4	3+	4—	3—	2—	8	8
Lygus pratensis	Estival	1—	3+	1—	4—	1—	1—	1—	4	0	0	0	—	0	0	0	—
	Autumnal	0	1—	1—	0	30	1—	1—	0	17	0	9	0	—	0	0	0
	Jun. 12-Oct. 29	1—	2—	1—	2+	17	1—	1—	2—	9—	0	6	0	0	0	0	0
Dikraneura abnormis	Estival	0	0	0	0	0	0	0	0	6	40	18	—	0	0	0	—
	Autumnal	0	0	0	0	0	0	0	0	76	83	66	101	—	0	0	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	44	54	47	101	0	0	0	0
Anoecia graminis	Estival	0	0	0	0	0	0	0	0	11	0	3—	—	0	0	0	—
	Autumnal	0	0	0	0	0	0	0	0	161	1	35	0	—	0	0	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	0	0	78	1—	22	0	0	0	0	0
Crematogaster lineolata	Estival	4—	3+	3+	1+	2	2	1—	1—	13	9	13	—	3—	0	0	—
	Autumnal	1—	1—	4—	1	1—	1	3	3—	1—	4—	2—	17	—	13	55	28
	Jun. 12-Oct. 29	2—	2	3+	1+	1+	3—	2—	2—	8	7	6	17	3—	4—	18	28
Prenolepis imparis	Estival	0	1—	0	0	1	3+	3+	1	1	6	20	—	3—	3+	0	—
	Autumnal	1—	0	0	0	0	0	1—	4—	78	4—	32	3	—	0	0	3—
	Jun. 12-Oct. 29	1—	1—	0	0	1—	2+	2+	3—	39	5	27	3	3—	2+	0	3—
Leiobunum sp.	Estival	0	0	0	0	0	0	1—	0	1—	1—	2	—	0	0	0	—
	Autumnal	0	0	0	0	0	0	0	1—	0	1—	0	1	—	0	1	0
	Jun. 12-Oct. 29	0	0	0	0	0	0	1—	1—	1—	1—	1—	1	0	0	1—	0
Blissus leucopterus	Estival	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	—
	Autumnal	1—	1—	0	0	3+	0	1—	0	0	0	1—	0	0	0	0	0
	Jun. 12-Oct. 29	1—	1—	0	0	2—	0	1—	0	0	0	1—	0	0	0	0	0
Piesma cinerea	Estival	1—	1—	0	0	0	0	0	0	0	1—	1—	0	0	1—	0	—
	Autumnal	1—	1—	0	0	1—	1—	0	0	4—	2—	3	0	—	2+	0	0
	Jun. 12-Oct. 29	1—	1—	0	0	1—	1—	0	0	2	1—	2	0	0	1—	0	0

The Spiders of Wisconsin*

Herbert W. Levi and Howard M. Field
University of Wisconsin, Madison

The purpose of this paper is 1) to add to the knowledge of the distribution of spiders by listing those occurring within the State of Wisconsin and the localities in which they occur, and 2) to aid in the identification of spiders in this region.

ACKNOWLEDGEMENTS

The authors extend their thanks to Drs. Lowrie and Elder for the use of their collections, and to Sister M. Melanie and her enthusiastic students; to Mrs. L. Levi, Mr. R. Hunt, Miss R. Schiferl, Miss K. E. Dorney, and to many others who contributed spiders to this collection. The senior author is indebted to Prof. L. E. Noland and to Prof. N. C. Fassett of the University of Wisconsin whose encouragement made possible a collecting trip through Wisconsin in 1949. He was fortunate to examine Dr. D. C. Lowrie's collection, made in southeastern Wisconsin between 1938 and 1940. A small collection of spiders made by Dr. Wm. Elder about 1938 was found at the University of Wisconsin. Acknowledgement is due to Dr. A. Archer, Miss E. Bryant, Dr. B. J. Kaston, Mr. W. Ivie and Dr. H. K. Wallace, who have at various times helped with identifications; to Dr. R. V. Chamberlin for the loan of a specimen; to Mrs. C. Crocker for help with library work; to Dr. W. J. Gertsch who gave the senior author a great deal of time, help, and advice, and loaned many spiders under his care for use in making drawings.

Kaston's monograph of Connecticut spiders (1948) is the most useful aid in identifying spiders. Of the spiders found in Wisconsin and not in New England, some belong to the northern fauna, some to the western, a few to the southern, and a few are known only in this region. The female genital plates (epigyna) and palps of the males of these groups of spiders are here illustrated and references are given to descriptions in the literature (illustrations from Wisconsin specimens unless otherwise noted). Genera not listed by Kaston are referred to the point to which they will run out in his keys. The species are listed alphabetically under either the subfamily or the family to which they belong. Revision of groups of the theridiids and argiopids, by Archer (1950, 1951) and a recent decision by the International Commission of Zoological Nomenclature to validate Clerck's (1757) names, have unfortunately resulted in some changes of generic and specific names from those used by Kaston.

It is hoped that, armed with Kaston's monograph and this paper, it will be possible to determine the majority of Wisconsin spiders without too many difficulties. It should be kept in mind, however, that the spider fauna of this part of the country is not too well known and many spiders probably occur here which have not been listed in this paper, or which are not now known to biologists. For information on the biology of spiders, the reader is referred to Comstock (1940) and Gertsch (1949).

The records preceded by asterisks are those taken from H. M. Field's thesis (1938).

---

* Supported in part by the Research Committee of the Graduate School of the University of Wisconsin from funds supplied by the Wisconsin Alumni Research Foundation.

Class ARACHNIDA
Order ARANEAE

Suborder ORTHOGNATHA (Mygalomorphae)
ATYPIDAE—Purse-web Spiders

Atypus niger Hentz, 1852. Purse-web spider.—In maple basswood forest. GRANT Co.: Wyalusing State Park.

Suborder LABIDOGNATHA (Araneomorphae)

DYSDERIDAE

Dysdera crocata C. L. Koch, 1839.—Cosmopolitan, under boards in backyards. DANE Co.: Madison.

SCYTODIDAE (Sicariidae)

Scytodes thoracica (Latreille, 1804).—Cosmopolitan, in cellars. DANE Co.: Madison; OUTAGAMIE Co.: Appleton.

PHOLCIDAE—Cellar Spiders

Pholcus phalangioides (Fuesslin, 1775).—Long-bodied cellar spiders.—Cosmopolitan in cellars. CRAWFORD Co.: Eastman; Prarie du Chien; DANE Co.: *Cambridge; Madison; GRANT Co.: Boscobel.

Spermophora meridionalis Hentz, 1832.—Short-bodied cellar spider.—Dark corners in house. CRAWFORD Co.: Prairie du Chien; DANE Co.: *Cambridge; Madison.

THERIDIIDAE—Comb-footed Spiders

The result of a recent revision of this family by Archer (1950) necessitates that a number of changes in generic names be made. The species previously placed in the genus *Enoplognatha* are now placed in the genus *Theridion*. The Wisconsin theridiids placed by Kaston and other authors in the genus *Theridion* should be placed in the following genera:

1a. Abdomen with a small, distinct dorso-apical tubercle ..... *Cryptachaea*

1b. Abdomen lacking the dorso-apical tubercle 2

2a. Abdomen of female much higher than long, flattened behind. Male palpus having the cymbium with a long extension, whose length beyond the bulb is more than two-thirds the length of the bulb ..... *Henziectypus*

2b. Abdomen of female not higher than long, male palpus without such a long extension of the cymbium 3

3a. Abdomen white, except for a large black spot encircling the spinnerets and often a black spot in the middle of the dorsum ..... *Tholocco*

3b. Abdomen otherwise 4

4a. Abdomen above white to grey with dark chevrons on the posterior portion. Relatively large spiders 4-10 mm. in length ..... *Parasteatoda*

4b. Abdomen otherwise, of varied paterns. Small spiders mostly less than 4 mm. in length ..... *Allotheridion*

Allotheridion alabamense (Gertsch and Archer, 1942) (*Theridion alabamense* Kaston, 1948).—GRANT Co.: Wyalusing State Park.

A. albidum (Banks, 1895) (*Theridion albidum* Kaston, 1948).—Frequently in a rolled up leaf. DANE Co.: Madison; DOUGLAS Co.: Brule; GRANT Co.: Wyalusing State Park; VERNON Co.: Coon Valley; VILAS Co.: Eagle River; WALWORTH Co.: Lake Geneva.

A. differens (Emerton, 1882) (*Theridion differens* Kaston, 1948).—The webs are found in bushes. Fairly common.

A. fieldi (Levi, 1951) fig. 1 (*Theridion fieldi* Levi, 1951, Am. Mus. Nov. 1501:3, fig. 46).—On vegetation. BUFFALO Co.: Merrick State Park. CRAWFORD Co.: Prairie du Chien; DANE Co.: *Madison; GRANT Co.: Wyalusing State Park; KEWAUNEE Co.: Kewaunee; LA CROSSE Co.: *La Crosse; SAUK Co.: *Prairie du Sac; VILAS Co.: *Trout Lake.

A. frondeum (Hentz, 1850) (*Theridion frondeum* Kaston, 1948).—In low bushes. Common.

A. glaucescens (Becker, 1879) (*Theridion glaucescens* Kaston, 1948).— Low vegetation. BUFFALO Co.: Merrick State Park; BURNETT Co.: Riverside; DANE Co.: Madison; DOOR Co.: Potawatomi State Park; GRANT Co.: Wyalusing State Park; KEWAUNEE Co.: Algoma; SAUK Co.: Devil's Lake; TREMPEALEAU Co.: Perrott State Park; VERNON Co.: Wildcat Mountain; WAUSHARA Co.: Wautoma.

A. lyricum (Walckenaer, 1842) (*Theridion lyricum* Kaston, 1948).— GRANT Co.: Wyalusing State Park; JACKSON Co.: Castle Mound; JUNEAU Co.: Rocky Arbor Roadside Park; VERNON Co.: Wildcat Mountain.

A. murarium (Emerton, 1882) (*Theridion murarium* Kaston, 1948).—On low vegetation. Common.

A. zelotypum (Emerton, 1882) fig. 3 (*Theridion zelotypum* Kaston, 1948, in part).—In low branches of trees. BARRON Co.: Chetek; BAYFIELD Co.: Bayfield; La Pointe; DOOR Co.: Bailey's Harbor; KEWAUNEE Co.: Kewaunee; VILAS Co.: Trout Lake.

Ancylorrhanis hirsutum (Emerton, 1882).—In forest floor litter. DOOR Co.: Peninsula State Park (common).

Asagena americana Emerton, 1882.—Roadsides, in grass. Fairly common in southern Wisconsin and DOOR Co.; no records north of Vernon Co.

Conopistha trigona (Hentz, 1850).—GRANT Co.: Wyalusing State Park; JUNEAU Co.: Rocky Arbor Roadside Park; MANITOWOC Co.: Point Beach State Forest; POLK Co.: *St. Croix Falls; SAUK Co.: North Freedom.

Crustulina altera Gertsch and Archer, 1942.—Under stones and logs. DANE Co.: Madison; DOOR Co.: Potawatomi State Park, Peninsula State Park; FOND DU LAC Co.: Mauthe Lake; GRANT Co.: Wyalusing State Park; LA CROSSE Co.: *La Crosse; POLK Co.: *St. Croix Falls; VILAS Co.: *Trout Lake; WAUSHARA Co.: *Pine River, Wautoma.

Cryptachaea rupicola (Emerton, 1882) (*Theridion rupicola* Kaston, 1948).—GRANT Co.: Wyalusing State Park.

Ctenium banksi Kaston, 1946.—Under stones and boards. GRANT Co.: *Wyalusing State Park; IRON Co.: Kimball; MARATHON Co.: *Wausau; POLK Co.: St. Croix Falls; SAUK Co.: Sauk City; VILAS Co.: *Trout Lake.

C. eremophilus (Chamberlin, 1928).—BUFFALO Co.: Merrick State Park; GRANT Co.: Wyalusing State Park; MARATHON Co.: Lac du Bay.

C. longipalpus Kaston, 1946.—MARATHON Co.: Hogarty.

C. riparius (Keyserling, 1886).—Fairly common in leaf litter in northern Wisconsin.

Dipoena nigra (Emerton, 1882).—BAYFIELD Co.: Port Wing; BURNETT Co.: Riverside; DANE Co.: Madison; DOOR Co.: Potawatomi State Park; WALWORTH Co.: College Camp.

Euryopis argentea Emerton, 1882.—POLK Co.: St. Croix Falls.

E. limbata (Walckenaer, 1841) (*E. funebris* (Hentz, 1850)).—DANE Co.: Sauk City; DOUGLAS Co.: Pattison State Park.

E. californica Banks, 1904.—This western form is very similar to *E. limbata*, but differs in that the conductor of the male palp has an elbow while that of *E. limbata* is straight. On vegetation in fields. DANE Co.: Madison; PEPIN Co.: Pepin.

E. saukea Levi, 1951 figs. 2, 4, 6, Levi, H. W. 1951, Am. Mus. Nov. 1501:6 figs. 5-9.—DANE Co.: south of Sauk City.

Hentziectypus globosum (Hentz, 1850) (*Theridion globosum* Kaston, 1948).—JACKSON Co.: Castle Mound; MARINETTE Co.: Pembine; ONEIDA Co.: Rhinelander; WAUSHARA Co.: Wautoma.

Latrodectus mactans (Fabricius, 1775). Black widow spider.—This is the only spider known to be poisonous occurring in this state. The black widow, though found near houses in southern states, has been found in Wisconsin under logs in forests and fields, in rather natural surroundings. No well authenticated reports of spider bites from Wisconsin are known to the authors, despite newspaper stories of their occurrence. The bites probably were those of insects. BUFFALO Co.: *Fountain City (1937); CRAWFORD Co.: Gays Mills (1950); DANE Co.: *Madison (1936) and one spider in University Arboretum, Madison (1949); south of Sauk City (1938); ROCK Co.: *Milton (1936); SAUK Co.: *Parfrey's Glen (1935, 1936); Baxter's Hollow (1949); VERNON Co.: Wildcat Mountain (1949); WALWORTH Co.: *Lake Geneva (1938); WAUSHARA Co.: Wautoma.

Figs. 1-9.—1. *Allotheridion fieldi* (Levi), epigynum (female genital plate); 2. *Euryopis saukea* Levi, abdomen of male; 3. *Allotheridion zelotypum* (Emerton), epigynum; 4. *Euryopis saukea* Levi, palp, mesal view. 5. *Theridion sexpunctatum* Emerton, palp, ventral view (N. Y.); 6. *Euryopis saukea* Levi, palp, ventral view; 7. *Theridion aurantium* Emerton, epigynum; 8. *Theridion aurantium* Emerton, palp, ventral view (Ontario); 9. *Theridion sexpunctatum* Emerton, epigynum (N. Y).

Lithyphantes albomaculatus (DeGeer, 1778).—Under stones in sand. ADAMS Co.: *Friendship; DANE Co.: Madison; south of Sauk City; IOWA Co.: Arena; WAUSHARA Co.: *Pine River.

Parasteatoda tepidariorum (C. L. Koch, 1841) *Theridion tepidariorum* Kaston, 1948) House spider.—This cosmopolitan spider is found in and around buildings, rarely under logs. Very common.

Steatoda borealis (Hentz, 1850).—Under logs and on buildings. Very common.

Teutana triangulosa (Walckenaer, 1802).—On buildings. CRAWFORD Co.: Prairie du Chien (common); DANE Co.: Madison.

Theonoe stridula Crosby, 1906.—DANE Co.: *Madison; VILAS Co.: *Trout Lake.

Theridion aurantium Emerton, 1915, figs. 7, 8. Emerton, J. H., Trans. Conn. Acad. Sci. 20:137, pl. 1, fig. 2.—This species of *Theridion* is likely to key out to *Teutana* in Kaston. FOREST Co.: Laona.

T. marmoratum Hentz, 1850 fig. 11 (*Enoplognatha marmorata* Kaston, 1948 (in part), figs. 35, 41).—Underneath stones and boards. BAYFIELD Co.: Herbster; CLARK Co.: near Stanley; DANE Co.: Madison; MARATHON Co.: Wausau; VILAS Co.: Eagle River.

T. puritanum (Chamberlin and Ivie, 1942) fig. 12 (*Enoplognatha marmorata* Kaston, 1948 (in part), figs. 36, 42).—Underneath stones and boards. Fairly common.

T. rugosum (Emerton, 1909) (*Enoplognatha rugosa* Kaston, 1948).—Under leaves. VILAS Co.: *Trout Lake.

T. sexpunctatum Emerton, 1882 figs. 5, 9, 10, Emerton, J. H. 1882, Trans. Conn. Acad. Sci. 6:12. pl. 2, fig. 5.—This species of Theridion will key out to *Teutana* in Kaston. On undercover in forests. PRICE Co.: Memorial Grove in Chequamegon National Forest; SAUK Co.: *Prairie du Sac.

Theridula sphaerula (Hentz, 1850).—On low vegetation. DOUGLAS Co.: *Superior; LINCOLN Co.: Merrill; MONROE Co.: Wyeville; SAWYER Co.: *Lac Court Oreilles.

Tholocco unimaculatum (Emerton, 1882) (*Theridion unimaculatum* Kaston, 1948).—On undercover in woods. DANE Co.: *Madison; LINCOLN Co.: Merrill; ONEIDA Co.: Rhinelander; TAYLOR Co.: Chequamegon National Forest.

NESTICIDAE

Nesticus pallidus Emerton, 1875. In hemlock forest. VILAS Co.: Lac du Flambeau.

LINYPHIIDAE—Sheet-web Weavers

Bathyphantes alboventris (Banks, 1892) figs. 13, 14, 19 (*Diplostyla alboventris* Banks, 1892) Proc. Acad Nat. Sci. Phila. 1892, p. 43, fig. 31.—RICHLAND Co.: Rockbridge.

B. concolor (Wider, 1834).—Under debris and manure. CLARK Co.: *Colby, Worden Twshp.; DANE Co.: Madison; LANGLADE Co.: Polar; MARATHON Co.: Wausau, Nutterville; TREMPEALEAU Co.: Perrot State Park; WINNEBAGO Co.: *Oshkosh.

B. pallida (Banks, 1892).—In debris, frequently on streambanks. ASHLAND Co.: Copper Falls State Park; DANE Co.: *Madison; DOUGLAS Co.: Pattison State Park; FLORENCE Co.: Tipler; GRANT Co.: Wyalusing State Park; IOWA Co.: Spring Green; VERNON Co.: Wildcat Mountain.

B. tristis Banks, 1892 ?. Banks, N. 1892, Proc. Acad. Nat. Sci. Phila. 1892, p. 46, fig. 45.—MARATHON Co.: Nutterville.

Bathyphantoides brevis (Emerton, 1911).—DANE Co.: Madison.

Centromerus persoluta (O. P. Cambridge, 1875).—Fairly common in forest litter in northern Wisconsin.

C. sylvaticus (Blackwall, 1841).—Fairly common in forest litter.

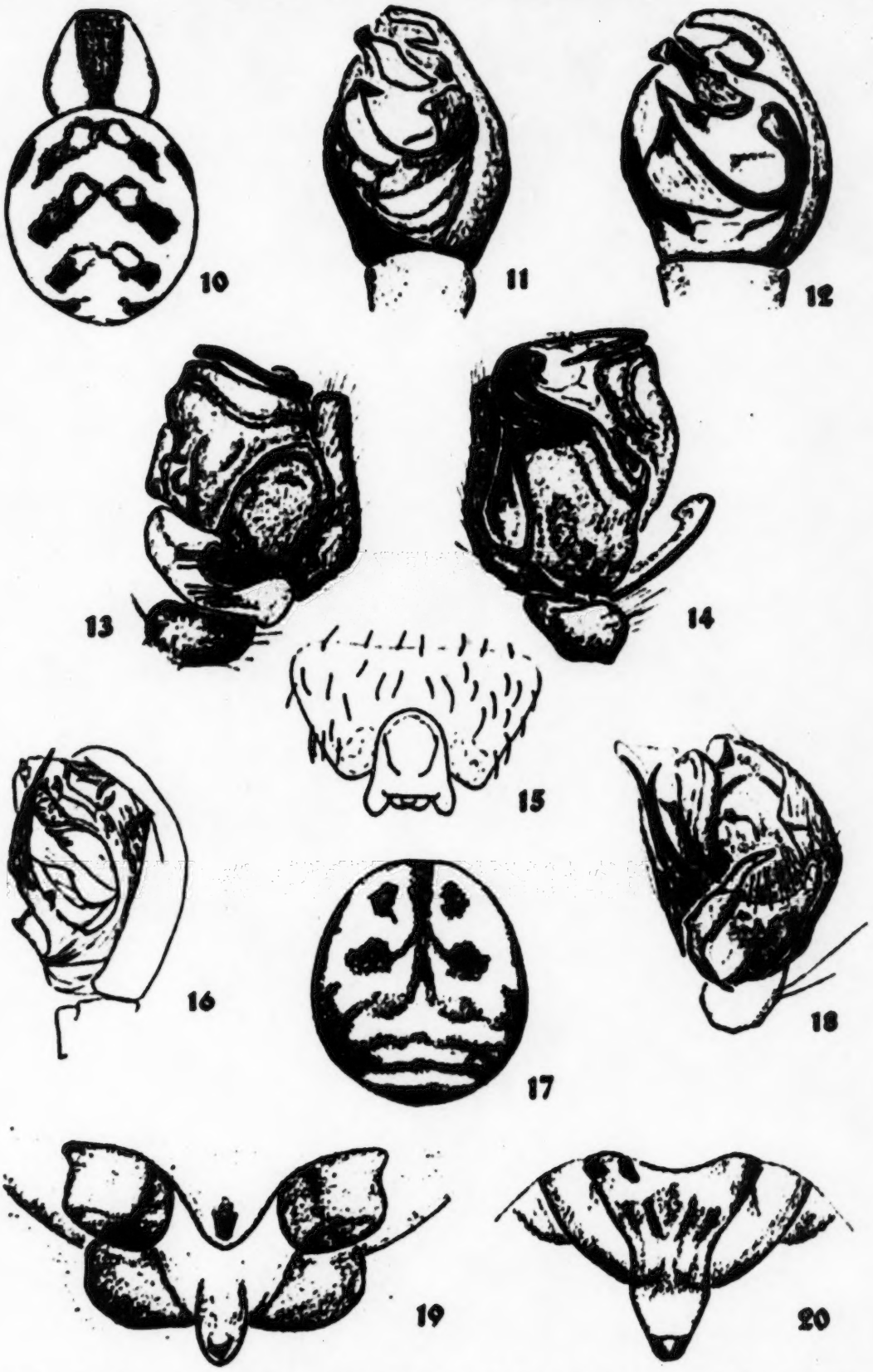
Drapetisca alteranda Chamberlin, 1909.—ASHLAND Co.: Copper Falls State Park; SAWYER Co.: *Lac Court Oreilles; VILAS Co.: *Trout Lake; *Partridge Lake.

Frontinella pyramitela (Walckenaer, 1841). Bowl and doily spider. (*F. communis*) (Hentz, 1850)).—The web is in shape of a cup, beneath which is a flat sheet about a meter above the ground (Comstock). Fairly common.

Helophora insignis (Blackwall, 1841).—The web is flat and in low vegetation (Comstock). Fairly common.

Lepthyphantes appalachia Chamberlin and Ivie, 1944.—In forest litter. DOOR Co.: Peninsula State Park.

L. furcata (Emerton, 1913) figs. 15, 16. Emerton, J. H. 1913, Trans. Conn. Acad.



Figs. 10-20.—10. *Theridion sexpunctatum* Emerton, dorsal view of female (N. Y.; 11. *Theridion marmoratum* Hentz, palp, ventral view (Minn.); 12. *Theridion puritanum* (Chamberlin and Ivie), palp, ventral view (Minn.); 13. *Bathyphantes alboventris* (Banks), palp, lateral view (Ohio); 14. *Bathyphantes alboventris* (Banks), palp, mesal view (Ohio); 15. *Lepthyphantes furcata* (Emerton), epigynum (after Zorsch); 16. *Lepthyphantes furcata* (Emerton), palp, lateral view (after Zorsch); 17. *Lepthyphantes subalpina* (Emerton), abdomen of female; 18. *Lepthyphantes subalpina* (Emerton), palp, lateral view; 19. *Bathyphantes alboventris* (Banks), epigynum; 20. *Lepthyphantes subalpina* (Emerton), epigynum.

Sci. 18:218, pl. 2, figs. 7b, 7c., Zorsch, H. M. 1937, Amer. Midl. Nat. 18(5):871, pl. 3, figs. 36-39.—MARATHON Co.: *Wausau.

L. leprosa (Ohlert, 1865).—DANE Co.: Madison; MARATHON Co.: Nutterville; VILAS Co.: *Trout Lake; WALWORTH Co.: College Camp; WINNEBAGO Co.: *Oshkosh.

L. nebulosa (Sundevall, 1830).—Fairly common.

L. subalpina (Emerton, 1882) figs. 17, 18, 20. Emerton, J. H. 1882, Trans. Conn. Acad. Sci. 6:70, pl. 22, fig. 3. Zorsch, H. M. 1937, Amer. Midl. Nat. 18(5):870, pl. 3, figs. 32-35.—Fairly common in northern Wisconsin, rarer in the southern part of the state.

L. zebra (Emerton, 1882).—Under leaves in woods. One had its web in a deer track in snow. DANE Co.: *Madison; DOOR Co.: Fish Creek; MARATHON Co.: Wausau; ONEIDA Co.: Woodruff, Gilmore Lake; SAWYER Co.: Flambeau State Forest.

Linyphia maculata Emerton, 1909.—DANE Co.: *Madison; DOOR Co.: Peninsula State Park; GRANT Co.: Wyalusing State Park; POLK Co.: *St. Croix Falls; WALWORTH Co.: College Camp.

L. marginata C. L. Koch, 1834. Filmy dome spider.—The web is dome shaped and is found among low plants in woods. Both sexes usually inhabit the same web. Very common.

L. waldea Chamberlin and Ivie, 1943.—The web is a flat sheet near the ground. DANE Co.: Madison; GRANT Co.: Wyalusing; SAUK Co.: *Prairie du Sac.

Meioneta sp.—ASHLAND Co.: Copper Falls State Park; MARATHON Co.: Nutterville.

Microneta complicata Banks, 1892, figs. 21, 22, 23. Banks, N. 1892, Proc. Acad. Nat. Sci. Phila. 1892: p. 47, pl. 2, fig. 50.—Forests. SHAWANO Co.: Neopit; VILAS Co.: Lac du Flambeau, Plum Lake.

M. viaria (Blackwall, 1841).—Leaf litter. MARATHON Co.: Rib Mountain; PORTAGE Co.: south of Stevens Point; ROCK Co.: near Edgerton; SHAWANO Co.: Neopit; TAYLOR Co.: Chequamegon National Forest.

M. sp.—DOUGLAS Co.: Brule.

Pityohyphantes costatus (Hentz, 1850). Hammock spider.—The web is a flat sheet, usually in woods. Very common.

Pusilla mandibulata (Emerton, 1882). Platform spider.—The webs are flat and near the ground (Emerton). BARRON Co.: *Rice Lake; DANE Co.: Madison; ONEIDA Co.: *Woodruff; VILAS Co.: *Trout Lake; WAUSHARA Co.: *Wild Rose.

Stemonyphantes lineatus (Linn., 1758).—DANE Co.: Madison; POLK Co.: *St. Croix Falls; WAUKESHA Co.: Waukesha.

Tapinopa bilineata Banks, 1893.—Under boards or close to the ground. DANE Co.: *Madison; JUNEAU Co.: Rocky Arbor Roadside Park; LA CROSSE Co.: *La Crosse; MARATHON Co.: Nutterville; Wausau.

Tennesseellum formicum (Emerton, 1882).—WAUKESHA Co.: Eagle.

MICRYPHANTIDAE (Erigonidae)—Dwarf Spiders

This very difficult group of minute spiders is only very incompletely known from Wisconsin. A number of females collected could not be identified because they were not accompanied by males, which are more easily determined. Though Kaston gives a description of many species occurring here, the papers of S. C. Bishop and C. R. Crosby will be the most useful in learning about this group.

Baryphyma longitarsum (Emerton, 1882).—MANITOWOC Co.: Point Beach State Forest.

Catabrithorax plumosus (Emerton, 1882). Crosby, C. R. and S. C. Bishop 1928, Bull. N. Y. State Mus. No. 278:70, figs. 97-101.—DANE Co.: Madison; DODGE Co.: Horicon; TREMPEALEAU Co.: Perrot State Park.

Ceraticelus atriceps (O. P. Cambridge, 1874).—BAYFIELD Co.: Port Wing.

C. emertoni (O. P. Cambridge, 1874).—On low vegetation in meadows and light woods. BURNETT Co.: Webster; DANE Co.: Madison; near Sauk City; MARQUETTE Co.: Endeavor; POLK Co.: St. Croix Falls.

C. fissiceps (O. P. Cambridge, 1874).—Collected by sweeping herbaceous vegetation in forests. Very common.

C. laetabilis (O. P. Cambridge, 1874).—On herb layer in forests. CHIPPEWA Co.: Brunet Island State Park; DOOR Co.: Peninsula State Park; MARATHON Co.: Rib Mountain; PRICE Co.: Memorial Grove in Chequamegon National Forest.

C. laetus (O. P. Cambridge, 1874).—Sifting litter. SAWYER Co.: Flambeau State Forest.

C. limnologicus Crosby and Bishop, 1925 (?). Crosby, C. R. and S. C. Bishop 1925, N. Y. State Mus. Bull. No. 264:32, figs. 61-65.—MARQUETTE Co.: Westfield (in dry oak woods).

C. minutus (Emerton, 1882).—On herb layer in forests. DOOR Co.: Peninsula State Park; PRICE Co.: Memorial Grove in Chequamegon National Forest; SAWYER Co.: Flambeau State Forest; VILAS Co.: *Lac du Flambeau.

Ceratinella brunnea Emerton, 1882.—On log in moist woods. MARATHON Co.: Rib Mountain.

Ceratinops annulipes (Banks, 1892). Crosby, C. R. and S. C. Bishop 1933, Ann. Ent. Soc Am. 26:109, figs. 1-5.—DANE Co.: Madison.

C. lata (Emerton, 1882).—CLARK Co.: near Stanley.

C. rugosa (Emerton, 1909).—MARATHON Co.: Rib Mountain.

Ceratinopsidis formosa (Banks, 1892). Bishop, S. C. and C. R. Crosby 1930, Jour. N. Y. Ent. Soc. 38:29, figs. 39-42.—DANE Co.: Madison; MONROE Co.: near Coon Valley (very abundant).

Ceratinopsis auriculata Emerton, 1909.—WALWORTH Co.: Lake Geneva.

C. nigriceps Emerton, 1882.—LINCOLN Co.: Merrill.

C. purpurescens (Keyserling, 1886). Bishop, S. C. and C. R. Crosby 1930, Jour. N. Y. Ent. Soc. 38:25, figs. 31-35. GRANT Co.: Wyalusing State Park; MONROE Co.: Coon Valley; RICHLAND Co.: south of Gotham.

Cornicularia clavicornis Emerton, 1882. Crosby, C. R. and S. C. Bishop 1931, Jour. N. Y. Ent. Soc. 39(3):365-366, figs. 18-23.—FOREST Co.: Lacna.

C. communis Emerton, 1882.—DANE Co.: *Madison; MARATHON Co.: Lac du Bay (?).

C. indirecta (O. P. Cambridge, 1874).—DANE Co.: *Madison.

C. minuta Emerton, 1882.—MARATHON Co.: Rib Mountain.

C. pallida Emerton, 1882.—DANE Co.: Madison in Bascom Woods.

Diplocephalus cristatus (Blackwall, 1833). Bishop, S. C. and C. R. Crosby 1935, Jour. N. Y. Ent. Soc. 43:239, figs. 42-43.—WINNEBAGO Co.: *Oshkosh.

Dismodicus decemoculatus (Emerton, 1882). Crosby, C. R. and S. C. Bishop 1933, Ann. Ent. Soc, Am. 26:149, figs. 165-169.—FLORENCE Co.: Tipler.

Eperigone index (Emerton, 1914). Crosby and Bishop, 1928, New York State Mus. Bull., No. 278, p. 52, figs. 117-120. In sphagnum.—TAYLOR Co.: Chequamegon National Forest near Medford.

E. maculata (Banks, 1892).—Common in forest litter.

E. trilobata (Emerton, 1882).—DANE Co.: Madison.

Eridantes erigonoides (Emerton, 1882). Crosby, C. R. and S. C. Bishop 1933, Ann. Ent. Soc. Am. 26:146, figs. 150-158.—ASHLAND Co.: Copper Falls State Park; DANE Co.: Madison; WALWORTH Co.: Sugar Creek; Lake Geneva.

E. utibilis Crosby and Bishop, 1933. Crosby, C. R. and S. C. Bishop 1933, Ann. Ent. Soc. Am. 26:148, figs. 159-164.—DOUGLAS Co.: Pattison State Park.

Erigone atra Blackwall, 1833.—GRANT Co.: Wyalusing.

E. blaesa Crosby and Bishop, 1928. Crosby, C. R. and S. C. Bishop 1928, Bull. N. Y. State Mus. 278:22, figs. 26-31.—DANE Co.: Madison; MARATHON Co.: Knowlton.

E. dentigera O. P. Cambridge, 1874.—Near water. DANE Co.: Madison; FLORENCE Co.: Tipler; GRANT Co.: Wyalusing State Park; WALWORTH Co.: Delavan, Lake Geneva, Sugar Creek.

Floricomus plumalis (Crosby), 1925.—DOOR Co.: Peninsula State Park.

Gnathonaroides pedalis (Emerton, 1923). Bishop, S. C. and C. R. Crosby 1938, Jour. N. Y. Ent. Soc. 46:84, figs. 65-66.—In leaf litter. DANE Co.: Madison.

Gonatium rubens (Blackwall, 1833).—In woods. MARATHON Co.: Eau Claire Dells County Park; MARINETTE Co.; VERNON Co.: Coon Valley; Wildcat Mountain.

Grammonota pictilis (O. P. Cambridge, 1875).—DOUGLAS Co.: Brule; WAUSHARA Co.: Wautoma.

G. vittata Barrows, 1919. Bishop, S. C. and C. R. Crosby 1932, Jour. N. Y. Ent. Soc. 40:412, figs. 50-52.—WALWORTH Co.: Lyons.

Hormathion limnatum Crosby and Bishop, 1933. Crosby, C. R. and S. C. Bishop 1933, Ann. Ent. Soc. Am. 26:161, figs. 205-210.—MARATHON Co.: Nutterville.

Hybocoptus cymbadentatus Crosby and Bishop, 1935. Crosby, C. R. and S. C. Bishop 1935, Ent. News 46:125, figs. 1-4.—In sphagnum. SAWYER Co.: Flambeau State Forest.

Hypselistes florens (O. P. Cambridge, 1875).—In high grass and ground vegetation of light woods. Common.

Minyriolus arenarius (Emerton, 1911). Crosby, C. R. and S. C. Bishop 1933, Ann. Ent. Soc. Am. 26:136, figs. 110-115.—DANE Co.: Madison.

M. castaneus (Emerton, 1882).—DANE Co.: Madison.

Oedothorax trilobatus (Banks, 1896). Bishop, S. C. and C. R. Crosby 1935, Jour. N. Y. Ent. Soc. 43:268, figs. 79-84.—VILAS Co.: *Trout Lake.

Origanates rostratus (Emerton, 1882).—SAUK Co.: Devil's Lake.

Sciastes terrestris (Emerton, 1882).—MARATHON Co.: Rib Mountain.

Scylaceus pallidus (Emerton, 1882).—In forest litter. DOOR Co.: Peninsula State Park.

Sisicus penifusiferus Bishop and Crosby, 1938. Bishop, S. C. and C. R. Crosby 1938, Jour. N. Y. Ent. Soc. 46:62, figs. 12-13.—In forest litter. DOOR Co.: Peninsula State Park; MARATHON Co.: Rib Mountain; SAWYER Co.: Flambeau State Forest.

Souessa spinifera (O. P. Cambridge, 1874).—Sifting leaves. SAWYER Co.: Flambeau State Forest.

Sougambus bostoniensis (Emerton, 1882).—MARATHON Co.: Wausau.

Soulgas corticarius (Emerton, 1909).—PRICE Co.: Memorial Grove in Chequamegon National Forest.

Tapinocyba simplex (Emerton, 1882).—Crosby, C. R. and S. C. Bishop 1933, Ann. Ent. Soc. Am. 26:123, figs. 59-63.—MANITOWOC Co.: Point Beach State Forest; LINCOLN Co.: Merrill.

Tmeticus ornatus (Emerton, 1914). Bishop, S. C. and C. R. Crosby 1935, Jour. N. Y. Ent. Soc. 43:227. figs. 22-26.—DANE Co.: Madison.

Tunagyna debilis (Banks, 1892)—Sifting leaves. SAWYER Co.: Flambeau State Forest.

Walckenaera vigilax (Blackwall, 1853).—BAYFIELD Co.: Herbster; CRAWFORD Co.: Prairie du Chien; FLORENCE Co.: Tipler; WALWORTH Co.: Sugar Creek.

EPEIRIDAE—Orb Weavers

American authors usually combine this and the following two families (Theridiosomatidae and Tetragnathidae), under the family name, ARGIOPIDAE. Most members of this family catch their prey in an orb web.

ARGIOPINAE—Argiopes

Both the species of *Argiope* may be of economic importance During an outbreak of grasshoppers in central Wisconsin in 1949, these abundant spiders were observed to capture and swathe in silk large numbers of grasshoppers.

Argiope aurantia Lucas, 1833. Orange argiope.—In high grass. Very common.

A. trifasciata (Forskål, 1775). Banded argiope.—In high grass. Very common.

Gea heptagon (Hentz, 1847) figs. 24, 25, 27. Comstock, J. 1940, The Spiderbook p. 457. McCook, H. C. 1893, American Spiders 3:208.—SAUK Co.: *Prairie du Sac.

EPEIRINAE

Acanthepeira stellata (Walckenaer, 1805). Star-bellied orb weaver.—In grassy roadsides. BURNETT Co.: Webster; DANE Co.: Madison; DOOR Co.: Peninsula State Park; OCONTO Co.: Machickanee County Forest; RICHLAND Co.: west of Gotham.

Aculepeira sp. figs. 26, 28. (*Epeira carbonaria* McCook, 1893), American Spiders 3:157, (*Aculepeira carbonaria* Levi, 1951), Am. Mus. Nov. 1501:11.—The genus *Aculepeira* keys out to *Epeira* in Kaston's key to the genera of this subfamily. "Wisconsin" (McCook). This may be the *A. verae* Chamberlin and Ivie, 1942, Bull. Univ. Utah 32(13), Biol. Ser. 7(1):75, figs. 215-216.

Araneus corticarius (Emerton, 1884) fig. 32.—MARATHON Co.: Mosinée; VILAS Co.: *Trout Lake.

Figs. 21-32.—21. *Microneta complicata* Banks, epigynum (locality ?); 22. *Microneta complicata* Banks, palp, ventral view; 23. *Microneta complicata* Banks, palp, dorsal view; 24. *Gea heptagon* (Hentz), palp, ventral view (Texas); 25. *Gea heptagon* (Hentz), abdomen of female (Texas); 26. *Aculepeira verae* Chamberlin and Ivie, palp, ventral view (Colo.); 27. *Gea heptagon* (Hentz), epigynum (Texas); 28. *Aculepeira verae* Chamberlin and Ivie, epigynum (Mont.); 29. *Araneus gemmoides* Chamberlin and Ivie, epigynum; 30. *Araneus gemmoides* Chamberlin and Ivie, palp, ventral view; 31. *Araneus gemmoides* Chamberlin and Ivie, abdomen of imm. female; 32. *Araneus corticarius* (Emerton), palp, mesal view (N. Y.).

A. diadematus Clerck, 1757. Cross spider.—"Wisconsin" (McCook).

A. gemmoides Chamberlin and Ivie, 1935, figs. 29, 30, 31, Chamberlin, R. V. and W. Ivie, 1935, Bull. Univ. Utah 26(4). Biol. Ser. 2(8):22.—On farm buildings. Probably fairly common in southern Wisconsin, north to Marathon Co.

A. nordmanni (Thorell, 1870).—BAYFIELD CO.: *La Pointe; DOOR CO.: *Bailey's Harbor; Ephraim; DOUGLAS CO.: *Superior; ONEIDA CO.: *Three Lakes; VILAS CO.: Eagle River, *Trout Lake.

A. marmoreus Clerck, 1757 (*Epeira raji* Kaston, 1948). Spectacled spider.—In woods. Very common.

A. solitarius (Emerton, 1884). "Wisconsin" (McCook). DOOR CO.: Ephraim; MONROE CO.: near Coon Valley; VILAS CO.: *Trout Lake; WALWORTH CO.: Lake Geneva.

A. thaddeus (Hentz, 1847) (*Epeira thaddeus* Kaston, 1948) Lattice spider.—"Wisconsin" (McCook). Miss Alma Sherman collected a specimen in Wisconsin; the locality is unknown.

A. trifolium (Hentz, 1847) (*Epeira trifolium* Kaston, 1948). Shamrock orb weaver. In high grass. Common.

Araniella displicata (Hentz, 1847) (*Epeira displicata* Kaston, 1948).—Meadows. Very common.

Cercidia prominens (Westring, 1851). DANE CO.: *Madison.

Conepeira glyphica Archer, 1951, figs. 33, 34. Archer, A. 1951, Am. Mus. Nov. 1502:17, fig. 56. Type locality: VERNON CO.: Wildcat Mountain.

C. mayo (McCook, 1893) fig 35. McCook, H. C. 1893. American Spiders 3:157. "Wisconsin" (McCook). JEFFERSON CO.: *Lake Ripley; LA CROSSE CO.: *La Crosse.

Cyclosa conica (Pallas, 1772). In light woods. Fairly common.

C. turbinata (Walckenaer, 1841). "Wisconsin" (McCook).

Epeira cornuta (Clerck, 1757) (*E. foliata* Kaston, 1948). Furrow spider.—On buildings. Common.

E. patagiata (Clerck, 1757) (*E. dumetorum* Kaston, 1948).—On buildings. Very common.

E. sericata (Clerck, 1757) (*E. undata* Kaston, 1948). Gray cross spider.—On buildings. BUFFALO CO.: Alma; DANE CO.: Madison; DOOR CO.: *Bailey's Harbor; Fish Creek. MARATHON CO.: Wausau; MILWAUKEE CO.: *Milwaukee; Lake.

Eustala anastera (Walckenaer, 1841). In shrubbery. Common.

Larinia borealis Banks, 1894.—DANE CO.: *Madison; POLK CO.: St. Croix Falls (Archer); WALWORTH CO.: East Troy.

Mangora gibberosa (Hentz, 1847).—Roadsides and fields. Common.

M. placida (Hentz, 1847).—Fields and groundcover in light woods. Common.

Metepeira labyrinthica (Hentz, 1847).—This species can be told from the following one by its light coxae and the presence of a longitudinal white line on the sternum. RACINE CO.: Burlington.

M. palustris Chamberlin and Ivie, 1942.—This species can be told from the preceding by its black trochanters, coxae and sternum. PORTAGE CO.: Stevens Point. SAWYER CO.: *Lac Court Oreilles.

Neoscona arabesca (Walckenaer, 1837).—In fields, shrubbery and on shrubs in light woods. Very common.

N. minima F. O. P. Cambridge, 1904.—Usually found together with *N. arabesca*. There is some doubt in the authors' minds as to the validity of the species. DODGE CO.: Horicon; FLORENCE CO.: Tipler; FOND DU LAC CO.: Mauthe Lake; FOREST CO.: Laona; MARATHON CO.: Knowlton.

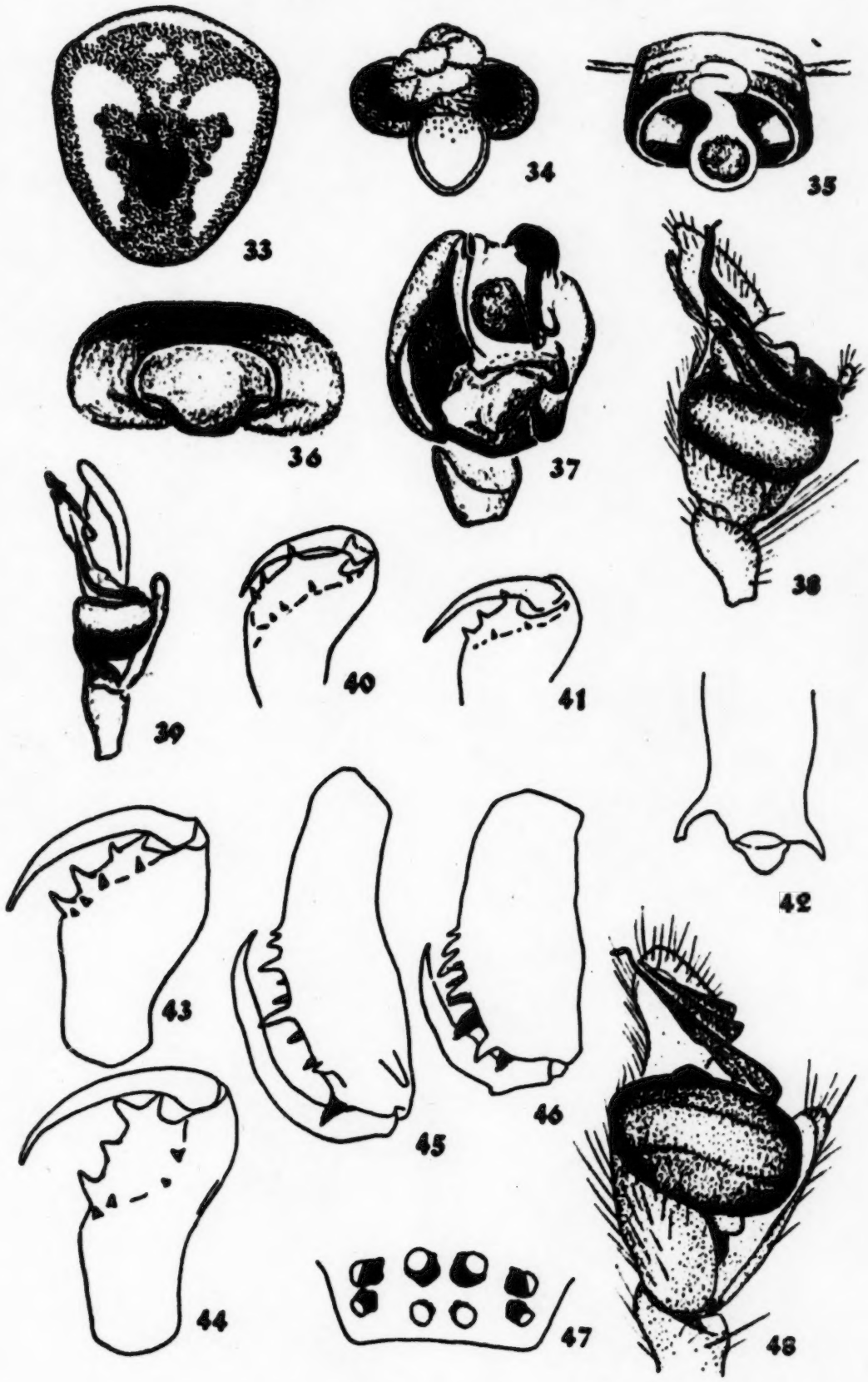
N. pratensis (Hentz, 1847).—DANE CO.: Madison; ROCK CO.: *Milton.

N. sacra (Walckenaer, 1841). Domicile orb weaver.—On shrubs and trees. CRAWFORD CO.: Eastman; Prairie du Chien; DANE CO.: Madison; JACKSON CO.: Castle Mound Roadside Park; JEFFERSON CO.: Lake Mills; KENOSHA CO.: Salem; RACINE CO.: Burlington; ROCK CO.: *Milton; WALWORTH CO.: La Grange.

Singa pratensis Emerton, 1884—BAYFIELD CO.: *Bayfield; SAWYER CO.: *Lac Court Oreilles; VILAS CO.: *Irving Lake; *Trout Lake.

S. variabilis Emerton, 1884.—DANE CO.: *Madison; PRICE CO.: Memorial Grove in Chequamegon National Forest (?) VILAS CO.: Anvil Lake; *Trout Lake.

Verrucosa arenata (Walckenaer, 1837).—DANE CO.: *Madison.



Figs. 33-48.—33. *Conepeira glyphica* Archer, abdomen of female; 34. *Conepeira glyphica* Archer, epigynum; 35. *Conepeira mayo* (McCook), epigynum (after McCook); 36. *Zygiella montana* C. L. Koch, epigynum (Alberta); 37. *Zygiella montana* C. L. Koch, palp, ventral view (Alberta); 38. *Pachygnatha kuratai* Levi, palp, lateral view (Ontario); 39. *Pachygnatha dorothea* McCook ?, palp, lateral view (Idaho); 40. *Pachygnatha dorothea* McCook ?, chelicera of male, posterior view (Idaho); 41. *Pachygnatha dorothea* McCook ?, chelicera of female, posterior view (Idaho); 42. *Tetragnatha harrodi* Levi,

Zygiella montana C. L. Koch, 1834, figs. 36, 37. Comstock, J. H. 1940, The Spider Book p. 471.—VILAS Co.: *Trout Lake.

METINAE

Meta menardii (Latreille, 1804). Cave dwelling orb weaver.—In caves, under rock crevices. DOOR Co.: Potawatomi State Park; GRANT Co.: *Wyalusing, Potosa; IRON Co.: Hurley.

GASTERACANTHINAE—Spiny-bellied orbweavers

Micrathena gracilis (Walckenaer, 1841).—Woods. GREEN Co.: New Glarus.

M. mitrata (Hentz, 1850).—Woods. "Wisconsin" (McCook); DOOR Co.: Peninsula State Park; GREEN Co.: New Glarus; MONROE Co.: near Coon Valley; VERNON Co.: Coon Valley, Wildcat Mountain.

M. sagittata (Walckenaer, 1841).—Fields, gardens and woods. CRAWFORD Co.: Gays Mills; DANE Co.: Madison; MONROE Co.: near Coon Valley; RICHLAND Co.: Rockbridge.

THERIDIOSOMATIDAE

Theridiosoma radiosum (McCook, 1881) (*T. gemmosum* Kaston, 1948). Ray spider.—DOUGLAS Co.: Brule; GRANT Co.: Wyalusing; SAUK Co.: *Prairie du Sac.

TETRAGNATHIDAE

Leucauge venusta (Walckenaer, 1837). Orchard spider.—Shrubbery and trees. This spider is locally very abundant. DANE Co.: Madison; GRANT Co.: Wyalusing State Park; JEFFERSON Co.: Lake Mills; RACINE Co.: Burlington; RICHLAND Co.: Rockbridge; SAUK Co.: Baraboo; WALWORTH Co.: La Grange, Lake Geneva; WAUKESHA Co.: Eagle.

Mimognatha foxi (McCook, 1894).—TREMPEALEAU Co.: Perrot State Park.

Pachygnatha dorothea McCook, 1893 ?. Thick-jawed spider, figs. 39, 40, 41. Bryant 1933, Bull. Mus. Comp. Zool. 74(6):176, figs. 37, 41.—DANE Co.: *Madison.

P. kuratai Levi, 1951, figs. 38, 43, 44. Levi, H. W. 1951, Am. Mus. Nov. 1501:15, figs. 29-31.—BARRON Co.: Rice Lake; DANE Co.: Madison; IRON Co.: Hurley; SHEBOYGAN Co.: *Waldo; VILAS Co.: *Trout Lake.

Tetragnatha banksi McCook, 1893 (*T. seneca* Seeley, 1928 of many authors).—Near water in meadows. "Wisconsin" (McCook). BUFFALO Co.: Merrick State Park; DANE Co.: *Madison, Mazomanie; MARATHON Co.: Mosinee; RACINE Co.: Tichigan Lake; VILAS Co.: *Trout Lake; WINNEBAGO Co.: *Oshkosh.

T. caudata Emerton, 1884.—Meadows, marshes. COLUMBUS Co.: Columbus; DANE Co.: *Madison; DODGE Co.: Horicon; GRANT Co.: *Wyalusing; MARATHON Co.: Knowlton; ONEIDA Co.: Lake Tomahawk; SAWYER Co.: *Lac Court Oreilles; WALWORTH Co.: Lyons.

T. elongata Walckenaer, 1805. Stilt-legged spider.—This, the largest of the tetragnathas, frequently builds its web over water. Common.

T. harrodi Levi, 1951, figs. 42, 45, 46, 47, 48. Levi, H. W. 1951, Am. Mus. Nov. 1501:17, figs. 32-37.—FLORENCE Co.: Tipler; RICHLAND Co.: Gotham (?).

T. laboriosa Hentz, 1850.—In tall grass, frequently away from water. Very common.

T. pallescens F. O. P. Cambridge, 1903.—Near water. DANE Co.: Madison; MANITOWOC Co.: Point Beach State Forest; MARATHON Co.: Knowlton; ROCK Co.: Edgerton; TREMPEALEAU Co.: Perrott State Park; VILAS Co.: *Trout Lake; WALWORTH Co.: Lyons, Lake Como; WAUSHARA Co.: *Wild Rose.

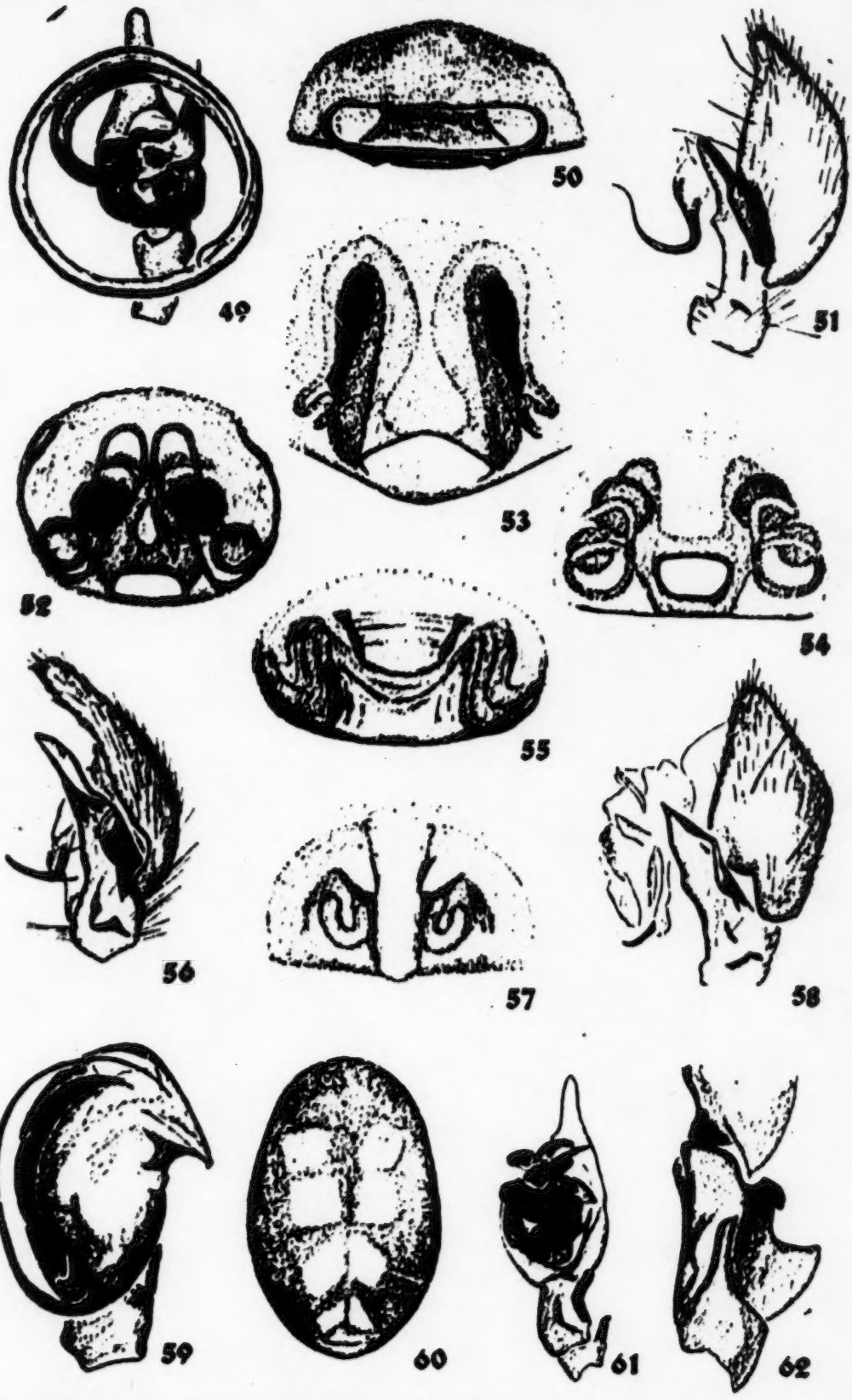
T. straminea Emerton, 1884.—Near water. DANE Co.: Madison; DOUGLAS Co.: Brule; LINCOLN Co.: Merrill; TAYLOR Co.: Chequamegon National Forest; WALWORTH Co.: Fontana, College Camp.

T. vermiformis Emerton, 1884.—"Wisconsin" (McCook).

T. versicolor Walckenaer, 1841.—Wet places, even in woods. Common.

---

chelicera of male, lateral view; 43. *Pachygnatha kuratai* Levi, chelicera of female, posterior view (Ontario); 44. *Pachygnatha kuratai* Levi, chelicera of male, posterior view (Ontario); 45. *Tetragnatha harrodi* Levi, chelicera of male, anterior view; 46. *Tetragnatha harrodi* Levi, chelicera of female, anterior view; 47. *Tetragnatha harrodi* Levi, eyes of female, anterior view; 48. *Tetragnatha harrodi* Levi, palp, lateral view.



Figs. 49-62.—49. *Agelenopsis oklahoma* (Gertsch), palp, ventral view; 50. *Agelenopsis oklahoma* (Gertsch), epigynum (after Chamberlin and Ivie); 51. *Cicurina lowriei* Levi, palp, lateral view; 52. *Cicurina arcuata* Keyserling, epigynum (N. Y.); 53. *Cicurina lowriei* Levi, epigynum; 54. *Cicurina itasca* Chamberlin and Ivie, epigynum; 55. *Coras lamellosus* (Keyserling), epigynum; 56. *Cicurina arcuata* Keyserling, palp, lateral view; 57. *Cryphoeca montana* Emerton, epigynum; 58. *Cicurina itasca* Chamberlin and Ivie, palp, lateral view; 59. *Cryphoeca montana* Emerton, palp, ventral view (N. Y.); 60. *Cryphoeca montana* Emerton, abdomen of female; 61. *Coras lamellosus* (Keyserling), palp, ventral view; 62. *Coras lamellosus* (Keyserling), patella and tibia of palp, lateral view.

MIMETIDAE

Ero leonina (Hentz, 1850) (*E. furcata* Kaston, 1948).—DANE Co.: *Madison; MARATHON Co.: *Wausau; POLK Co.: *St. Croix Falls; VILAS Co.: *Partridge Lake.

Mimetus epeiroides Emerton, 1882.—On shrubbery. DANE Co.: Madison.

M. notius Chamberlin, 1923.—JUNEAU Co.: SW quarter 19N 3E; MARATHON Co.: Wausau.

M. puritanus Chamberlin, 1923.—On shrubbery. DANE Co.: *Madison; JACKSON Co.: Castle Mound; POLK Co.: St .Croix Falls; SAUK Co.: *Prairie du Sac; WALWORTH Co.: Lake Geneva; WAUSHARA Co.: *Pine River.

AGELENIDAE—Funnel-web Weavers

Many members of this family build funnel-like webs on the ground and in vegetation; others are found under bark or under logs.

Agelenopsis naevia (Walckenaer, 1805). Grass spider.—CRAWFORD Co.: Prairie du Chien; GRANT Co.: Wyalusing State Park; TREMPEALEAU Co.; Perrot State Park.

A. oklahoma (Gertsch, 1936), figs. 49, 50. Gertsch, W. 1936, Am. Mus. Nov. 852:12, figs. 4-5. Chamberlin, R. V. and W. Ivie, 1941, Ann. Ent. Soc. Am. 34(3):591, figs. 7, 19, 37.—CRAWFORD Co.: Prairie du Chien.

*A. pensylvanica** (C. L. Koch, 1843). Grass spider.—In grass and around buildings; abundant wherever it occurs. CRAWFORD Co.: Eastman, Prairie du Chien; DANE Co.: Madison; GRANT Co.: Wyalusing State Park, Platteville; WAUSHARA Co.: Wautoma (?).

A. potteri (Blackwall, 1846). Grass spider.—In grass and around buildings. Very common.

A. utahana (Chamberlin and Ivie, 1933).—In ground cover in woods and forests. Very common.

Cicurina arcuata Keyserling, 1887, figs. 52, 56. Chamberlin, R. V. and W. Ivie 1940, Bull. Univ. Utah 30(18):, Biol. Ser. 5(9):63, figs. 46, 47, 84, 85.—DANE Co.: Madison.

C. brevis (Emerton, 1889).—*C. minnesota* Chamberlin and Ivie 1940, is probably a synonym or a variety of this species. On herbs and litter in woods and forests. Fairly common.

C. itasca Chamberlin and Ivie, 1940, figs. 54, 58. Chamberlin, R. V. and W. Ivie 1940, Bull. Univ. Utah 30(18), Biol. Ser. 5(9):62, fig. 48 ♀. Levi, H. W. 1951, Am. Mus. Nov. 1501:19, fig. 18 ♂.—In ground cover in forests. DOOR Co.: Fish Creek, Peninsula State Park; PRICE Co.: Chequamegon National Forest; SHAWANO Co.: Neopit.

C. lowrici Levi, 1951, figs. 51, 53. Levi, H. W. 1951, Am. Mus. Nov. 1501:20, figs. 17, 19.—This species, though much like *C. brevis*, can easily be distinguished since its anterior median eyes are much larger than its posterior median eyes. DANE Co.: Madison; WALWORTH Co.: Lake Geneva.

Coras lamellosus (Keyserling, 1887), figs. 55, 61, 62. Muma, M. H. 1946, Am. Mus. Nov. 1329:6, figs. 7, 27-30.—In crevices and hollow trees. Fairly common.

C. montanus (Emerton, 1889).—In crevices, hollow trees, and under bark. Fairly common.

Cryphoeca montana Emerton, 1909, figs. 57, 59, 60. Emerton, J. H. 1909, Trans. Conn. Acad. Sci. 14:222, pl. 8, fig. 4.—The genus *Cryphoeca* runs out to *Cicurina* in Kaston's key of this family. ASHLAND Co.: Copper Falls State Park; DOUGLAS Co.: Pattison State Park; FLORENCE Co.: Tipler; PRICE Co.: Chequamegon National Forest; SAUK Co.: *Prairie du Sac; SHAWANO Co.: Neopit.

Tegenaria domestica (Clerck, 1757) (*T. derhamii* Kaston, 1948).—In hollow trees, crevices and cellars. Cosmopolitan.

---

* This species has frequently been misspelled *A. pennsylvanica*, because it was assumed that Koch had made an error in orthography. See Egler, F. E. 1941, The orthography of "pensylvanicus." Rhodora 43:220-221.

Wadotes calcaratus (Keyserling, 1887).—Hollow trees, crevices. DOOR Co.: Peninsula State Park; FOREST Co.: Laona; OCONTO Co.: Machickanee County Forest; ONEIDA Co.: *Three Lakes; SHAWANO Co.: Neopit.

HAHNIIDAE

Hahnia cinerea Emerton, 1890—Leaf litter. JEFFERSON Co.: south of Cambridge; PORTAGE Co.: south of Stevens Point.

Neoantistea agilis (Keyserling, 1887).—Under stones and moist leaves in woods. DANE Co.: Madison; LA CROSSE Co.: Timber Coulee in Coon Valley.

N. riparia (Keyserling, 1887) (*N. radula* Kaston, 1948).—Kaston differentiates between the western *N. riparia* whose posterior median eyes are smaller than the anterior median eyes, while the eyes of *N. radula* are of the same size. Since Wisconsin specimens, even spiders from the same locality collected together, vary considerably in this characteristic, it is assumed that only one species is involved. Fairly common.

PISAURIDAE—Nursery-web Spiders

These are hunting spiders that do not make a web to catch their prey.

Dapanus mirus (Walckenaer, 1837).—On herbs and shrubs in woods. Common.

Dolomedes scopularis C. L. Koch, 1848 (*D. triton sexpunctatus* Kaston, 1948).—Frequently collected on water. CLARK Co.: Owen; CRAWFORD Co.: Prairie du Chien; DANE Co.: Madison; GREEN LAKE Co.: Green Lake; SAUK Co.: *Devil's Lake; VILAS Co.: *Trout Lake; WALWORTH Co.: Lyons; WAUKESHA Co.: Genesee Depot.

D. scriptus Hentz, 1845. Giant fishing spider.—Near water. Common.

D. striatus Giebel, 1869.—Near water. BAYFIELD Co.: Port Wing; DANE Co.: *Cambridge, Madison.

D. tenebrosus Hentz, 1844. Giant fishing spider.—Near water. Common.

LYCOSIDAE—Wolf Spiders

Most members of this family hunt their prey by pursuing it.

Arctosa emertoni Gertsch, 1934.—CRAWFORD Co.: Prairie du Chien; TREMPEALEAU Co.: Perrot State Park; VILAS Co.: *Trout Lake.

A. littoralis (Hentz, 1844).—On sandy shores. DANE Co.: *Madison, Mazomanie (?); VILAS Co.: Eagle River, *Trout Lake; WAUSHARA Co.: Wautoma.

A. rubicunda (Keyserling, 1876).—BURNETT Co.: *Siren; VILAS Co.: *Trout Lake.

Geolycosa missouriensis (Banks, 1895). Burrowing wolf spider. figs. 63, 64. Wallace H. K. 1942, Amer. Midl. Nat. 27(1): 13, figs. 1, 2, 34, 50, 51, 76, 86, 97, 107.—CRAWFORD Co.: Paririe du Chien; DANE Co.: south of Sauk City; SAUK Co.: Spring Green (Wallace).

Lycosa aspersa Hentz, 1844.—Fields. CRAWFORD Co.: Gays Mills, Prairie du Chien; DANE Co.: *Madison; OCONTO Co.: *Suring; WAUSHARA Co.: Wautoma.

L. avara (Keyserling, 1876).—Under logs and stones. DANE Co.: Madison; SAUK Co.: Devil's Lake; ROCK Co.: Edgerton.

L. avida Walckenaer, 1837.—Under stones in fields. CLARK Co.: near Stanley; CRAWFORD Co.: Gays Mills; DANE Co.: Madison; JEFFERSON Co.: *Lake Ripley; LA CROSSE Co.: *La Crosse; OCONTO Co.: *Suring; ROCK Co.: *Edgerton; WALWORTH Co.: Delavan, Lake Geneva, Laverdale.

L. baltimoriana (Keyserling, 1876).—CRAWFORD Co.: Prairie du Chien (common); WAUSHARA Co.: Wautoma.

L. carolinensis Walckenaer, 1837.—This is the largest of our wolf spiders. Two of the records were the result of accidental trappings, one spider being taken from a barrel, the other from a window-well. CRAWFORD Co.: Prairie du Chien; DANE Co.: *Madison, Waunakee; MARATHON Co.: Wausau.

L. frondicola Emerton, 1885.—In woods among litter. Fairly common.

L. gulosa Walckenaer, 1837.—In forests. Common.

L. helluo Walckenaer, 1837.—In fields and woods, frequently collected under stones. One of the specimens was dug out of a several inches long burrow. Fairly common.

L. pratensis Emerton, 1885 (*Trochosa pratensis* Kaston, 1948).—Under stones in woods and fields. Common.

Pardosa distincta (Blackwall, 1846).—Fields and woods. DANE Co.: Madison; DOOR Co.: Peninsula State Park; FLORENCE Co.: Tipler; GRANT Co.: Wyalusing State Park; MARATHON Co.: Halder; PIERCE Co.: *Ellsworth; SHEBOYGAN Co.:

Kettle Moraine State Forest; VERNON Co.: Coon Valley; VILAS Co.: *Trout Lake; WAUSHARA Co.: Wautoma.

P. fuscula (Thorell, 1872), figs. 65, 69.—FLORENCE Co.: Tipler.

P. groenlandica (Thorell, 1872) ?, figs. 66, 68.—Common among the stones of the shore of Green Bay. DOOR Co.: Ephraim, Peninsula State Park.

P. lapidicina Emerton, 1885.—DOOR Co.: Ephraim, Peninsula State Park; POLK Co.: *St. Croix Falls.

P. mackenziana (Keyserling, 1876).—Forests. ASHLAND Co.: Copper Falls State Park; BAYFIELD Co.: Port Wing; CLARK Co.: *Colby; DOOR Co.: Ephraim; FLORENCE Co.: Tipler; VERNON Co.: *De Soto; VILAS Co.: *Trout Lake; WAUSHARA Co.: Wautoma.

P. milvina (Hentz, 1844).—Fairly common.

P. modica (Blackwall, 1846)—CLARK Co.: near Stanley; DANE Co.: *Madison; ROCK Co.: *Edgerton; SAUK Co.: *Prairie du Sac.

P. moesta Banks, 1892.—Fairly common.

P. saxatilis (Hentz, 1844).—Fields. CRAWFORD Co.: Prairie du Chien; DANE Co.: Madison; GRANT Co.: Glen Haven, *Wyalusing State Park; IRON Co.: Hurley; JEFFERSON Co.: *Lake Ripley; SAUK Co.: Prairie du Sac; WAUPACA Co.: Clintonville.

P. xerampelina (Keyserling, 1876).—In logs in woods. Fairly common.

Pirata arenicola Emerton, 1909.—BUFFALO Co.: Merrick State Park; DANE Co.: *Madison; GRANT Co.: *Wyalusing; SAWYER Co.: *Lac Court Oreilles; TREMPEALEAU Co.: Perrot State Park; VERNON Co.: Coon Valley; WAUSHARA Co.: Wautoma.

P. insularis Emerton, 1885.—Near water. Fairly common.

P. maculatus Emerton, 1909.—CHIPPEWA Co.: Brunet Island; RICHLAND Co.: West of Gotham; VERNON Co.: Coon Valley.

P. minutus Emerton, 1885.—Usually in woods. Fairly common.

P. montanus Emerton, 1885.—In forests, frequently on hills. Fairly common.

P. piratica (Clerck, 1757).—BARRON Co.: *Rice Lake; DANE Co.: *Madison; DOUGLAS Co.: Brule; FLORENCE Co.: Tipler; IRON Co.: Hurley; SAWYER Co.: *Lac Court Oreilles; VILAS Co.: *Trout Lake; WALWORTH Co.: Lake Como, Lyons; WAUKESHA Co.: Genesee Depot; WAUSHARA Co.: Wautoma.

Schizocosa bilineata (Emerton, 1885).—In fields. GRANT Co.: Wyalusing.

S. crassipalpis (Emerton, 1909).—DANE Co.: *Madison; SAUK Co.: *Prairie du Sac.

S. crassipes (Walckenaer, 1837).—Fields and woods. Common.

S. saltatrix (Hentz, 1844).—Fields. DANE Co.: Madison; GRANT Co.: Wyalusing; SAWYER Co.: *Lac Court Oreilles; WAUSHARA Co.: *Pine River; Wautoma.

Tarentula aculeata (Clerck, 1757).—BARRON Co.: Chetek; FLORENCE Co.: Tipler.

Trabea aurantiaca (Emerton, 1885).—Woods. CLARK Co.: near Stanley; JUNEAU Co.: Rocky Arbor Roadside Park; LA CROSSE Co.: *La Crosse; VILAS Co.: *Trout Lake; WALWORTH Co.: Lake Geneva.

OXYOPIDAE—Lynx Spiders

Oxyopes salticus Hentz, 1845. Lynx spider.—In high grass. DANE Co.: Madison; near Sauk City; GRANT Co.: *Wyalusing State Park; LAFAYETTE Co.: Wiota; VERNON Co.: *De Soto; WALWORTH Co.: Fontana; Lake Geneva; Sugar Creek; WOOD Co.: Marshfield.

O. sp. (*O. scalaris* Hentz, 1845 ?).—BURNETT Co.: *Siren

GNAPHOSIDAE—Running Spiders

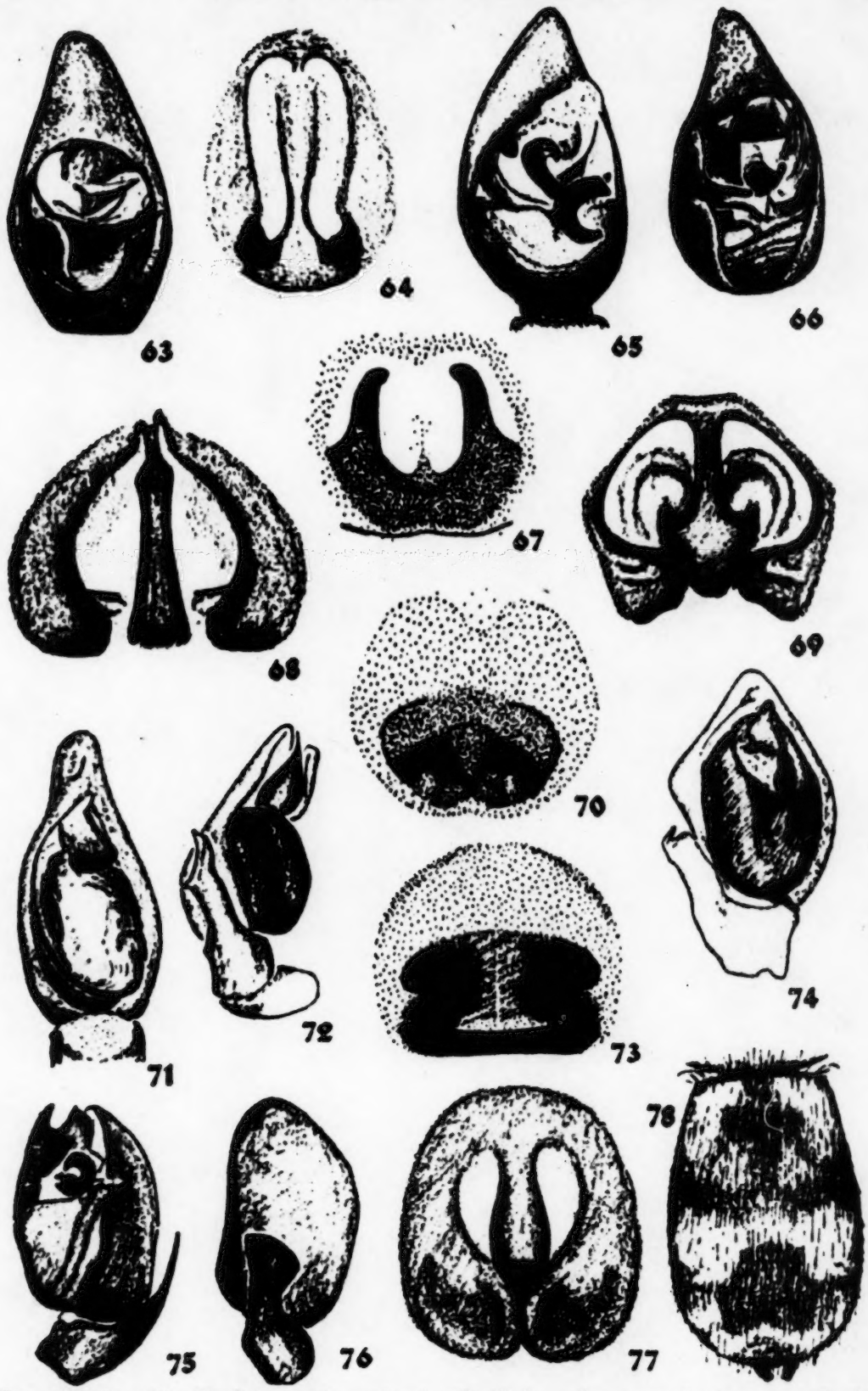
The members of this family are ground spiders, being nocturnal for the most part. During the day they may be found under stones and logs.

GNAPHOSINAE

Callilepis imbecilla (Keyserling, 1887).—ADAMS Co.: Roche a Cri Roadside Park; BUFFALO Co.: Alma; COLUMBIA Co.: Black Hawk Lookout; GRANT Co.: Wyalusing State Park; SAWYER Co.: *Lac Court Oreilles; SAUK Co.: *Prairie du Sac; WAUSHARA Co.: Wautoma.

Gnaphosa fontinalis Keyserling, 1887.—GRANT Co.: Wyalusing; WALWORTH Co.: Lake Geneva.

G. muscorum (L. Koch, 1866).—Fairly common.



Figs. 63-78.—63. *Geolycosa missouriensis* (Banks), palp, ventral view; 64. *Geolycosa missouriensis* (Banks), epigynum; 65. *Pardosa fuscula* (Thorell), palp, ventral view (Alberta); 66. *Pardosa groenlandica* (Thorell), palp, ventral view (Minn.); 67. *Haplodrassus bicornis* (Emerton), epigynum; 68. *Pardosa groenlandica* (Thorell), epigynum; 69. *Pardosa fuscula* (Thorell), epigynum (Alberta); 70. *Nodocion melanie* Levi, epigynum; 71. *Scotophaeus loricatus* (L. Koch), palp, ventral view; 72. *Poecilochroa montana* Emerton, palp, mesal view; 73. *Poecilochroa montana* Emerton, epigynum; 74. *Nodocion melanie* Levi, palp, ventral view; 75. *Haplodrassus bicornis* (Emerton), palp, lateral view; 76. *Haplodrassus bicornis* (Emerton), palp, dorsal view; 77. *Scotophaeus loricatus* (L. Koch), epigynum; 78. *Poecilochroa montana* Emerton, abdomen of female.

G. parvula Banks, 1896.—BAYFIELD Co.: Herbster, Port Wing; DANE Co.: Madison; OCONTO Co.: *Suring; PIERCE Co.: *Ellsworth; SAUK Co.: *Prairie du Sac; VILAS Co.: *Trout Lake; WAUPACA Co.: Clintonville.

G. sericata (L. Koch, 1866).—IOWA Co.: Arena.

DRASSINAE

Cesonia bilineata (Hentz, 1847).—On sandy beaches. WALWORTH Co.: Lake Geneva; WAUSHARA Co.: Wautoma, *Pine River.

Drassodes auriculoides Barrows, 1919.—SAUK Co.: near Baraboo.

D. neglectus (Keyserling, 1887).—In woods. Fairly common.

Drassyllus depressus (Emerton, 1890).—DANE Co.: Madison.

D. fallens Chamberlin, 1922.—GRANT Co.: Wyalusing State Park.

D. niger (Banks, 1911).—DANE Co.: Madison.

D. rufulus (Banks, 1892).—GRANT Co.: *Platteville; SAUK Co.: *Prairie du Sac.

D. virginianus Chamberlin, 1922.—WALWORTH Co.: Lake Geneva.

Haplodrassus bicornis (Emerton, 1909), figs. 67, 75, 76. Emerton, J. H. 1909, Trans. Conn. Acad. Sci. 14:218, pl. 9, fig. 2.—POLK Co.: St. Croix Falls.

H. hiemalis (Emerton, 1909).—BAYFIELD Co.: Port Wing; DANE Co.: *Madison.

H. signifer (C. L. Koch, 1839).—DANE Co.: Madison; LINCOLN Co.: Merrill; VILAS Co.: *Trout Lake.

Herpyllus vasifer (Walckenaer, 1805). Parson spider.—Under stones and boards, frequently on or in buildings. Common.

Nodocion melanie Levi, 1951, figs. 70, 74. Levi, H. W. 1951, Am. Mus. Nov. 1501:20-22.—The genus *Nodocion* will key out to 9b. *Zelotes* (in part) in Kaston's key to the Drassinae. CRAWFORD Co.: Prairie du Chien; SAUK Co.: *Baraboo; WAUSHARA Co.: Wautoma.

Poecilochroa capulata (Walckenaer, 1837) (*P. variegata* (Hentz, 1847)) (*Sergiolus variegatus* Kaston, 1948).—DOOR Co.: Potawatomi State Park; GRANT Co.: Wyalusing State Park; LA CROSSE Co.: *La Crosse; ROCK Co.: Edgerton; SAUK Co.: Parfrey's Glen; *Prairie du Sac; WALWORTH Co.: Delavan.

P. famula (Chamberlin, 1922) (*Sergiolus famulus* Kaston, 1948).—DANE Co.: *Madison; VILAS Co.: *Trout Lake.

P. montana Emerton, 1890, figs. 72, 73, 78. Emerton, J. H. 1890, Trans. Conn. Acad. Sci. 8:175, pl. 4, fig. 2.—*Poecilochroa montana* keys out to 9b *Zelotes* (in part) in Kaston's key to the Drassinae. CRAWFORD Co.: Prairie du Chien; DANE Co.: Madison; FLORENCE Co.: Tipler.

Scotophaeus loricatus (L. Koch, 1866), figs. 71, 77. (*Sostogeus zygethus* Chamberlin, R. V. and W. J. Gertsch, 1940, Am. Mus. Nov. 1068:1, figs. 1-4). (*Sostogeus zygethus* Levi, H. W. 1951, Am. Mus. Nov. 1501:26).—The genus *Scotophaeus* keys out to either 2a *Sosticus* or to 5a *Geodrassus* in Kaston's key to the Drassinae. CRAWFORD Co.: Prairie due Chien (several specimens); DANE Co.: Madison; GRANT Co.: Glen Haven; MARATHON Co.: Wausau.

Sosticus insularis (Banks, 1895).—CRAWFORD Co.: Eastman; Prairie du Chien; FOND DU LAC Co.: Ripon.

Zelotes hentzi Barrows, 1945.—WAUSHARA Co.: Wautoma.

Z. puritanus Chamberlin, 1922.—VILAS Co.: Sayner.

Z. subterraneus (C. L. Koch, 1839).—Under stones and leaves. Common.

CLUBIONIDAE—Sack Spiders

CLUBIONINAE

On vegetation in trees and shrubbery, frequently in a sacklike web in a rolled up leaf.

Clubiona abbotii L. Koch, 1866.—Fairly common.

C. canadensis Emerton, 1890.—BAYFIELD Co.: *Bayfield, *La Pointe; DANE Co.: *Madison; DOOR Co.: *Bailey's Harbor, Peninsula State Park; DOUGLAS Co.: Pattison State Park; FLORENCE Co.: Tipler; VILAS Co.: *Trout Lake.

C. chippewa Gertsch, 1941, fig. 83. Gertsch, W. J. 1941, Am. Mus. Nov. 1148:16.—POLK Co.: St. Croix Falls (holotype); FLORENCE Co.: Tipler.

C. kastoni Gertsch, 1941.—MARATHON Co.: Halder.

C. mixta Emerton, 1890.—DANE Co.: Madison; GRANT Co.: Fennimore; RACINE Co.: Tichigan Lake.

C. moesta Banks, 1896.—DANE Co.: *Madison; DOUGLAS Co.: *Superior; FOREST

Co.: *Argonne; MANITOWOC Co.: Point Beach State Forest; ONEIDA Co.: Woodboro; SAUK Co.: *Prairie du Sac; VILAS Co.: *Trout Lake; WALWORTH Co.: Lake Geneva.

C. obesa Hentz, 1847.—BAYFIELD Co.: *La Pointe; DANE Co.: Madison; DOOR Co.: Peninsula State Park; GRANT Co.: Wyalusing State Park; LINCOLN Co.: Merrill; RACINE Co.: Tichigan Lake; SAWYER Co.: *Lac Court Oreilles; VILAS Co.: *Trout Lake; WALWORTH Co.: Fontana.

C. pallens Hentz, 1847.—Fairly common.

C. pygmaea Banks, 1892.—DANE Co.: Madison; DOUGLAS Co.: *Superior; PIERCE Co.: *Ellsworth; SAUK Co.: *Parfrey's Glen.

C. riparia L. Koch, 1866. ? might be *C. praematura* Emerton, 1909.—BAYFIELD Co.: *Bayfield; DANE Co.: *Madison; DOOR Co.: *Bailey's Harbor; DOUGLAS Co.: *Superior; MARATHON Co.: *Wausau; SAWYER Co.: *Lac Court Oreilles; VILAS Co.: *Trout Lake.

C. tibialis Emerton, 1890.—DANE Co.: Madison; MARATHON Co.: Knowlton.

CORINNINAE

Trachelas tranquillus (Hentz, 1847).—On the ground, frequently in buildings. CRAWFORD Co.: Prairie du Chien; DANE Co.: Madison; MILWAUKEE Co.: Milwaukee; POLK Co.: St. Croix Falls.

LIOCRANINAE

On vegetation or in logs.

Agroeca ornata Banks, 1892.—In leaf litter. Fairly common in northern Wisconsin.

A. pratensis Emerton, 1890.—BAYFIELD Co.: *La Pointe; DANE Co.: Madison; LA CROSSE Co.: *La Crosse; MARATHON Co.: Nutterville; PIERCE Co.: *Ellsworth; SAUK Co.: *Prairie du Sac; SAWYER Co.: *Lac Court Oreilles; VILAS Co.: *Trout Lake; WAUSHARA Co.: *Pine River.

Phrurotimpus alarius (Hentz, 1847).—DANE Co.: Madison; DOOR Co.: Peninsula State Park; GRANT Co.: Wyalusing State Park; POLK Co.: St. Croix Falls; WALWORTH Co.: La Grange.

P. borealis (Emerton, 1911).—ADAMS Co.: Roche a Cri Roadside Park; CLARK Co.: near Stanley; DANE Co.: *Madison; DOUGLAS Co.: Pattison State Park; FLORENCE Co.: Tipler; GRANT Co.: Wyalusing State Park; POLK Co.: *St. Croix Falls; SAUK Co.: *Prairie du Sac; SAWYER Co.: *Lac Court Oreilles.

Scotinella madisonia Levi, 1951, fig. 79. Levi, H. W. 1951, Am. Mus. Nov. 1501:27, figs. 23,27.—The genus *Phrurolithus* is synonymous with *Scotinella*. DANE Co.: Madison.

S. manitou Levi, 1951, figs. 81, 85. Levi, H. W. 1951, Am. Mus. Nov. 1501:28, figs. 24-26, 28.—DOUGLAS Co.: Pattison State Park; MARATHON Co.: Hogarty (in sphagnum).

S. minnetonka (Chamberlin and Gertsch, 1930), figs. 80, 88. Chamberlin, R. V. and W. J. Gertsch, 1930, Proc. Biol. Soc. Wash. 43:139, figs. 13-15.—In leaf litter. DOUGLAS Co.: Brule; KEWAUNEE Co.: Kewaunee; MARATHON Co.: Rib Mountain.

MICARIINAE

Under stones and leaves or rapidly running on the ground.

Castianeira cingulata (C. L. Koch, 1842).—Common.

C. descripta (Hentz, 1847).—DANE Co.: *Madison; DOOR Co.: Peninsula State Park, *Bailey's Harbor; LA CROSSE Co.: *La Crosse; MARATHON Co.: Knowlton, Rib Mountain; POLK Co.: St. Croix Falls; VILAS Co.: *Trout Lake.

C. longipalpus (Hentz, 1847).—Fairly common.

C. trilineata (Hentz, 1847).—RICHLAND Co.: Route 60 west of Gotham; WALWORTH Co.: Lake Como.

Micaria longipes Emerton, 1890.—MARATHON Co.: Wausau.

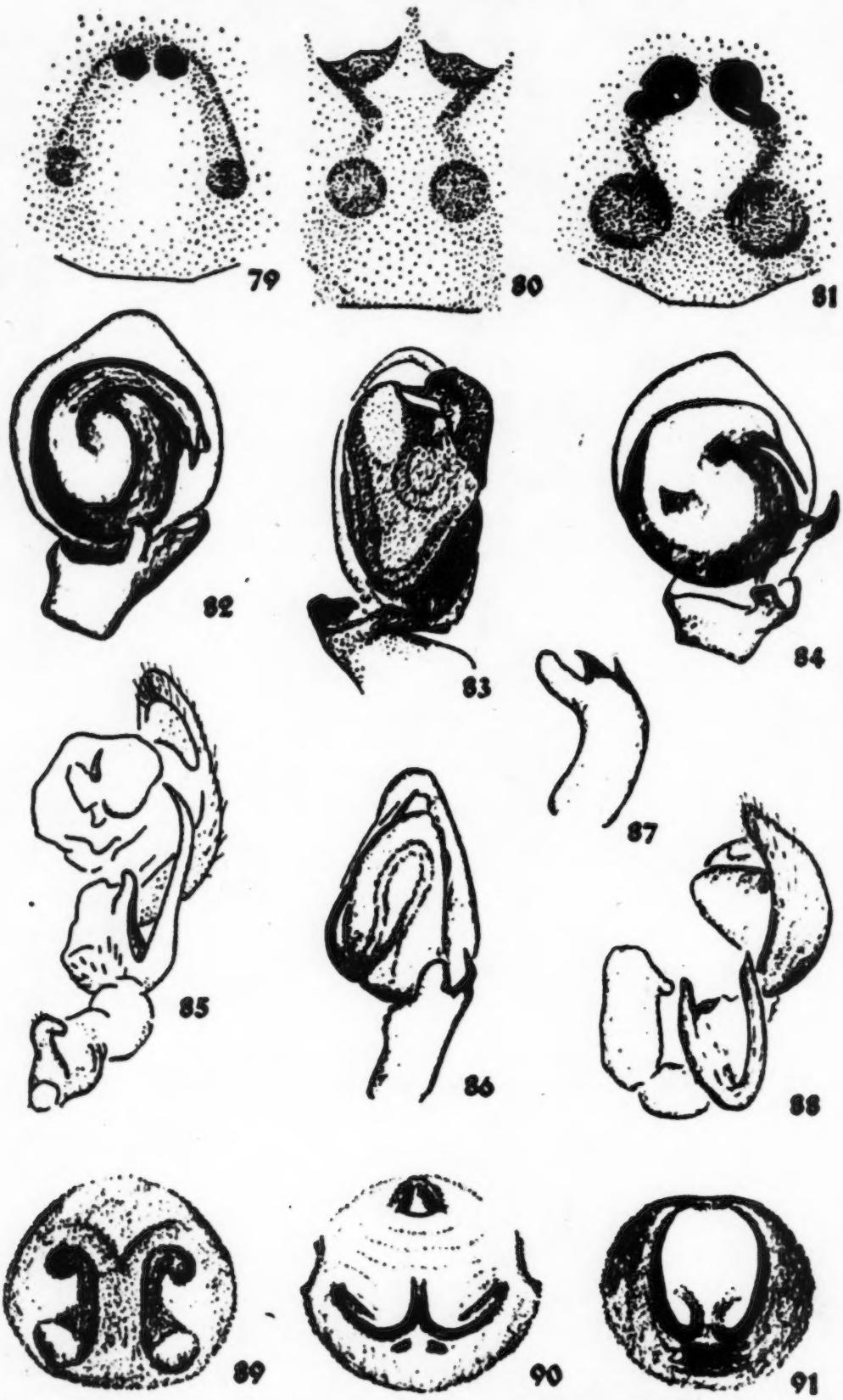
M. longispina Emerton, 1890.—DOUGLAS Co.: Pattison State Park.

M. montana Emerton, 1911.—CLARK Co.: near Stanley; FLORENCE Co.: Tipler; MARATHON Co.: Nutterville; RACINE Co.: Union Grove; SAUK Co.: *Wisconsin Dells.

ANYPHAENIDAE

Anyphaena celer (Hentz, 1847).—DANE Co.: Madison.

A. pectorosa L. Koch, 1866.—DANE Co.: Madison; GRANT Co.: Fennimore; JEFFERSON Co.: *Lake Ripley; WALWORTH Co.: Delavan; Lake Geneva.



Figs. 79-91.—79. *Scotinella madisonia* Levi, epigynum; 80. *Scotinella minnetonka* (Chamberlin and Gertsch), epigynum; 81. *Scotinella manitou* Levi, epigynum; 82. *Oxyptila modesta* (Scheffer), palp, ventral view (Ohio); 83. *Clubiona chippewa* Gertsch, palp ventral view; 84. *Xysticus lutulentus* Gertsch, palp, ventral view (Ontario); 85. *Scotinella manitou* Levi, palp, ventral view (bulb expanded); 86. *Philodromus oneida* Levi, palp, ventral view; 87. *Philodromus oneida* Levi, tibia of palp, lateral view. 88. *Scotinella minnetonka* (Chamberlin and Gertsch), palp, lateral view (Minn.); 89. *Philodromus oneida* Levi, epigynum; 90. *Oxyptila modesta* (Scheffer), epigynum (Ohio); 91. *Xysticus lutulentus* Gertsch, epigynum (Ontario).

Aysha gracilis (Hentz, 1847).—ADAMS Co.: Adams; DANE Co.: Madison; GRANT Co.: Wyalusing.

THOMISIDAE—Crab Spiders

The spiders belonging to this family do not make a web for capturing prey, but wait for it on flowers or bark.

MISUMENINAE

Coriarachne lenta (Walckenaer, 1837). (*C. versicolor* Keyserling, 1880)—In cracks of bark and on buildings. Fairly common.

Misumena vatia (Clerck, 1757) (*M. calycina* Kaston, 1948).—This spider may change its color to match the flower on which it sits. Common.

Misumenoides formosipes (Walckenaer, 1837) (*M. aleatorius* (Hentz, 1847)).—On flowers. Common.

Misumenops asperatus (Hentz, 1847).—This spider can change its color to match the flower on which it waits for prey. Very common.

M. oblongus (Keyserling, 1880).—On flowers. DANE Co.: *Madison; GRANT Co.: Fennimore; PIERCE Co.: *Ellsworth; SAWYER Co.: *Lac Court Oreilles; VILAS Co.: *Irving Lake; WALWORTH Co.: Lake Geneva.

Oxyptila americana Banks, 1895.—DANE Co.: *Madison; ROCK Co.: Edgerton, *Milton.

O. conspurcata Thorell, 1877.—DANE Co.: *Madison; DODGE Co.: Beaver Dam (Gertsch); SAUK Co.: *Prairie du Sac; VILAS Co.: *Trout Lake.

O. modesta (Scheffer, 1904), figs. 82, 90. Gertsch, W. J. 1939, Bull. Am. Mus. Nat. Hist. 76:340, figs. 104, 105, 127, 128.—DANE Co.: *Madison; GRANT Co.: *Wyalusing State Park; SAUK Co.: *Prairie du Sac; VILAS Co.: *Trout Lake.

Tmarus angulatus (Walckenaer, 1837).—In high grass. Fairly common.

Xysticus bicuspis Keyserling, 1887.—ADAMS Co.: Roche a Cri Roadside Park; DANE Co.: Madison.

X. elegans Keyserling, 1880.—Very common.

X. emertoni Keyserling, 1880.—FOREST Co.: *Argonne; IRON Co.: Hurley; SAWYER Co.: *Lac Court Oreilles.

X. fraternus Banks, 1895.—DANE Co.: Madison; CLARK Co.: Worden Twshp.; GRANT Co.: Wyalusing (Gertsch); SAUK Co.: *Prairie du Sac; VILAS Co.: *Trout Lake.

X. gulosus Keyserling, 1880.—On vegetation in fields or woods or under stones. Fairly common.

X. luctans (C. L. Koch, 1845).—BAYFIELD Co.: *Bayfield; DANE Co.: Madison; GRANT Co.: Platteville (Gertsch); MONROE Co.: Leon; WINNEBAGO Co.: *Oshkosh.

X. lutulentus Gertsch, 1934, figs. 84, 91. Gertsch, W. J. 1939, Bull. Am. Mus. Nat. Hist. 76:396, figs. 242, 243, 262.—DANE Co.: *Madison; DOUGLAS Co.: *Superior; SAWYER Co.: *Lac Court Oreilles.

X. ontariensis Emerton, 1919.—GRANT Co.: Platteville (Gertsch); POLK Co.: St. Croix Falls (Gertsch).

X. transversatus (Walckenaer, 1837) (*X. ferox* (Hentz, 1847)).—DANE Co.: Madison; GRANT Co.: Platteville; Wyalusing State Park; POLK Co.: *St. Croix Falls (Gertsch); WALWORTH Co.: Laverdale, Lake Como, Lake Geneva.

X. triguttatus Keyserling, 1880.—Fairly common.

X. tumefactus (Walckenaer, 1837) (*X. funestus* Keyserling, 1880).—CRAWFORD Co.: Prairie du Chien; DANE Co.: *Madison; GRANT Co.: Platteville; POLK Co.: *St. Croix Falls.

PHILODROMINAE

Philodromus abbotii Walckenaer, 1837 (*P. marxii* Keyserling, 1883).—GRANT Co.: Boscobel; Wyalusing; SAUK Co.: *Prairie du Sac; SHAWANO Co.: Keshena.

P. aureolus (Clerck, 1757).—Very common.

P. imbecillus Keyserling, 1880.—CRAWFORD Co.: Prarie du Chien; DANE Co.: Madison; WALWORTH Co.: College Camp.

P. infuscatus Keyserling, 1880—RICHLAND Co.: Rockbridge.

P. oneida Levi, 1951, figs. 86, 87, 89. Levi, H. W. 1951, Am. Mus. Nov. 1501:31, figs. 40-42.—ONEIDA Co.: Rhinelander.

P. pernix Blackwall, 1846.—Fairly common.

P. placidus Banks, 1892.—DANE Co.: *Madison; LAFAYETTE Co.: Darlington; PIERCE Co.: *Ellsworth.

P. rufus Walckenaer, 1825—Fairly common.

P. satullus Keyserling, 1880.—SAUK Co.: Sauk City; VERNON Co.: Coon Valley.

Thanatus formicinus (Clerck, 1757).—In grass. Common.

Tibellus maritimus (Menge, 1874).—DANE Co.: *Madison; DOUGLAS Co.: *Superior; FLORENCE Co.: Tipler; POLK Co.: *St. Croix Falls; SAUK Co.: *Prairie du Sac; TAYLOR Co.: Medford; WINNEBAGO Co.: *Oshkosh.

T. oblongus (Walckenaer, 1802).—Fields and roadsides. Very common.

SALTICIDAE—Jumping Spiders

Salticids are spiders that secure their prey by jumping on it.

Admestina tibialis (C. L. Koch, 1848).—"Wisconsin" (Peckham); DANE Co.: Madison; MARATHON Co.: *Wausau.

Ballus youngii Peckham, 1888.—"Pine Lake" (Peckham); KENOSHA Co.: Salem.

Evarcha hoyi (Peckham, 1883).—Fairly common.

Gertschia noxiosa (Hentz, 1850)?.—DANE Co.: *Madison.

Habrocestum pulex (Hentz, 1846).—Common.

Habronattus borealis (Banks, 1895).—MILWAUKEE Co.: Milwaukee; PEPIN Co.: Pepin.

H. decorus (Blackwall, 1846).—DANE Co.: Madison; LA CROSSE Co.: *La Crosse; VILAS Co.: Eagle River; *Trout Lake; WALWORTH Co.: Lake Como.

H. viridipes (Hentz, 1846).—"Wisconsin, common" (Peckham); SAWYER Co.: *Lac Court Oreilles.

Hasarius adansonii (Audouin, 1827).—DANE Co.: *Madison; SAUK Co.: *Prairie du Sac.

Hentzia ambigua (Walckenaer, 1837).—CHIPPEWA Co.: Brunet Island; FOND DU LAC Co.: Mauthe Lake; PIERCE Co.: Maiden Rock.

H. mitrata (Hentz, 1846).—"Wisconsin" (Peckham); CLARK Co.: Worden Twshp.; DANE Co.: *Madison.

Hyctia bina (Hentz), 1846.—DANE Co.: *Madison; SAWYER Co.: *Lac Court Oreilles.

H. pikei Peckham, 1888.—WALWORTH Co.: Lake Geneva.

Icius elegans (Hentz, 1846).—"Wisconsin" (Peckham); DANE Co.: *Madison, near Sauk City; DOOR Co.: *Sturgeon Bay; WALWORTH Co.: Lake Geneva.

I. fontanus Levi, 1951, figs. 93, 94, 95. Levi, H. W. 1951, Am. Mus. Nov. 1501:33, figs. 43-45.—WALWORTH Co.: Fontana.

I. hartii Emerton, 1891.—"Wisconsin" (Peckham); CRAWFORD Co.: Prairie du Chien; DANE Co.: *Madison; DODGE Co.: *Fox Lake; OCONTO Co.: *Suring; SAUK Co.: *Prairie du Sac; TREMPEALEAU Co.: Perrott State Park; WALWORTH Co.: College Camp.

I. similis Banks, 1895.—"Wisconsin" (Peckham); BAYFIELD Co.: Port Wing; DANE Co.: Madison; LINCOLN Co.: Corning; MANITOWOC Co.: Point Beach State Forest; ONEIDA Co.: Woodboro; WALWORTH Co.: College Camp, Lake Geneva, Sugar Creek.

Maevia inclemens (Walckenaer, 1837) (*M. vittata* (Hentz, 1845)).—Common.

Marpissa undata (De Geer, 1778).—CRAWFORD Co.: Prairie du Chien (very common); DANE Co.: *Waunakee; GRANT Co.: Boscobel; POLK Co.: *St. Croix Falls; SAUK Co.: Devil's Lake, *Prairie du Sac; WAUKESHA Co.: *Mukwonago.

Metacyrba taeniola (Hentz, 1846), figs. 96, 98. Peckham, G. W. and E. G. Peckham, 1909, Trans. Wisc. Acad. Sci. 16(1):486, pl. 39, fig. 5; pl. 40, fig. 4.—The genus *Metacyrba* will key out to 22a, *Hentzia* in Kaston's key to the genera of the Salticidae. "Wisconsin" (Peckham).

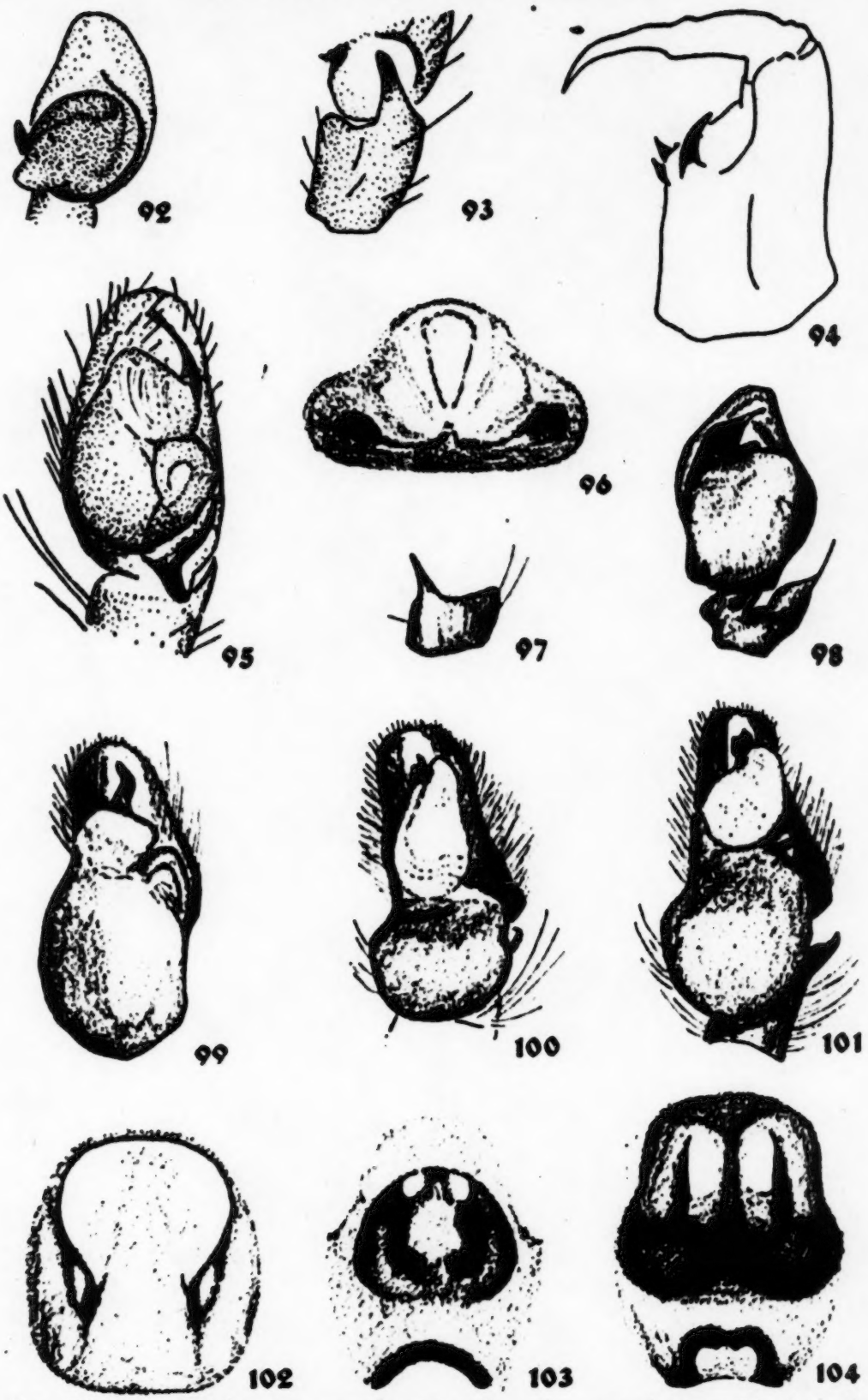
Metaphidippus canadensis (Banks, 1897).—SAUK Co.: *Prairie du Sac.

M. flavipedes (Peckham, 1881).—FOREST Co.: *Argonne; VILAS Co.: *Trout Lake.

M. insignis (Banks, 1892).—DANE Co.: Madison; GREEN Co.: York.

M. protervus (Walckenaer, 1837).—(*M. capitatus* (Hentz)), 1845. Very common.

Neon nellii Peckham, 1888.—DANE Co.: *Madison; DOOR Co.: Peninsula State Park; GRANT Co.: Fennimore, Wyalusing State Park; LINCOLN Co.: Merrill; MANITOWOC Co.: Point Beach State Forest.



Figs. 92-104.—92. *Sassacus aemulus* Gertsch, palp, ventral view; 93. *Icius fontanus* Levi, tibia of palp, lateral view; 94. *Icius fontanus* Levi, chelicera of male, posterior view; 95. *Icius fontanus* Levi, palp, ventral view (reconstructed from expanded bulb); 96. *Metacyrba taeniola* (Hentz), epigynum (Texas); 97. *Sassacus papenhoei* Peckham, tibia of palp, lateral view (Idaho); 98. *Metacyrba taeniola* (Hentz), palp, ventral view (Texas); 99. *Sassacus papenhoei* Peckham, palp, ventral view (Idaho); 100. *Phidippus apacheanus* Chamberlin and Gertsch, palp, ventral view; 101. *Phidippus altanus* Gertsch, palp, ventral view; 102. *Sassacus papenhoei* Peckham, epigynum; 103. *Phidippus apacheanus* Chamberlin and Gertsch, epigynum (Utah); 104. *Phidippus altanus* Gertsch, epigynum (Alberta).

Onondaga lineata (C. L. Koch, 1848).—"Wisconsin" (Peckham); DANE Co.: *Madison.

Paraphidippus marginatus (Walckenaer, 1837).—Very common.

Peckhamia picata (Hentz, 1846).—"Wisconsin" (Peckham), DANE Co.: Madison (?); DOOR Co.: Potawatomi State Park (?); WALWORTH Co.: Genoa City (?); WAUSHARA Co.: *Pine River.

Phidippus altanus Gertsch, 1934, figs. 101, 104. Gertsch, W. J. 1934, Am. Mus. Nov. 726:12, fig. 13.—MARATHON Co.: Wausau; ONEIDA Co.: Rhinelander; VILAS Co.: Eagle River.

P. apacheanus Chamberlin and Gertsch, 1929, figs. 100, 103. Chamberlin, R. V. and W. J. Gertsch, 1929, Jour. Ent. Zool. 21:109, figs. 46, 49.—SAUK Co.: Spring Green.

P. audax (Hentz, 1844).—In fields and houses. Several specimens were sent in by people believing they were black-widow spiders. Very common.

P. princeps (Peckham, 1883).—CRAWFORD Co.: Prairie du Chien; WALWORTH Co.: Lake Geneva; WOOD Co.: Marshfield.

P. purpuratus Keyserling, 1884.—DANE Co.: near Sauk City; POLK Co.: *St. Croix Falls; VILAS Co.: *Trout Lake.

P. rimator (Walckenaer, 1837) (*P. clarus* Keyserling, 1884).—Fairly common.

P. whitmanii Peckham, 1909.—LINCOLN Co.: Merrill; MILWAUKEE Co.: Milwaukee (Peckham); SAUK Co.: *Prairire du Sac; VILAS Co.: Anvil Lake; WAUSHARA Co.: Wautoma (?).

Phlegra fasciata (Hahn, 1831). Leopard spider.—"Wisconsin" (Peckham); POLK Co.: St. Croix Falls.

Salticus scenicus (Clerck, 1757). Zebra spider.—Is commonly seen crossing window panes, inside or outside of buildings. Common in southern Wisconsin; there are fewer records from northern part of the state.

Sassacus aemulus Gertsch, 1934, fig. 92. Gertsch, W. J. 1934, Am. Mus. Nov. 726:22, fig. 20.—The genus *Sassacus* keys out to 14 and does not go any further, unless possibly to 17a, *Agassa*, in Kaston's key to the Salticidae. DOUGLAS Co.: Brule.

S. papenhoei Peckham, 1895, figs. 97, 99, 102. Peckham, G. W. and E. C. Peckham, 1909, Trans. Wisc. Acad. Sci. 16(1):592, pl. 49, fig. 11.—WALWORTH Co.: Delavan.

Sitticus cursor Barrows, 1919, figs. 105, 106. Barrows, W. M. 1919, Ohio Jour. Sci. 19(6):359, fig. 8.—Roadside. IOWA Co.: Barneveld.

S. palustris (Peckham, 1883).—Fairly common.

S. striatus Emerton, 1911.—VILAS Co.: *Trout Lake.

Synemosyna lunata (Walckenaer, 1837) (*S. formica* Hentz, 1845).—"Wisconsin" (Peckham); DANE Co.: *Madison; GRANT Co.: Wyalusing State Park; PIERCE Co.: *Ellsworth; WALWORTH Co.: Delavan, Lake Geneva, Sugar Creek.

Thiodina sp.—The genus *Thiodina* will not key out further than to 2 in Kaston's key to the Salticidae, however it can be recognized easily by two pairs of bulbous hairs on the venter of the first tibia. MARATHON Co.: Wausau (probably introduced from California, or Arizona).

Zygoballus bettini Peckham, 1888.—"Wisconsin" (Peckham); FOND DU LAC Co.: Mauthe Lake; JEFFERSON Co.: Lake Mills; WALWORTH Co.: Lake Como.

Z. nervosus (Peckham, 1891).—BARRON Co.: *Rice Lake; CRAWFORD Co.: Prairie du Chien; DANE Co.: *Cambridge; *Madison; JEFFERSON Co.: Lake Mills; TREMPEALEAU Co.: Perrot State Park.

DICTYNIDAE—Hackled Band Weavers, Cribellate Spiders

Spiders of this group are commonly found in small webs on herbaceous plants, shrubbery or rolled up in leaves.

Argenna obesa Emerton, 1911.—RICHLAND Co.: Gotham.

Dictyna alias Chamberlin, 1948, figs. 110, 111. Chamberlin, R. V. 1948, Bull. Univ. Utah 38(15) Biol. Ser. 10(6):7.—PEPIN Co.: Pepin.

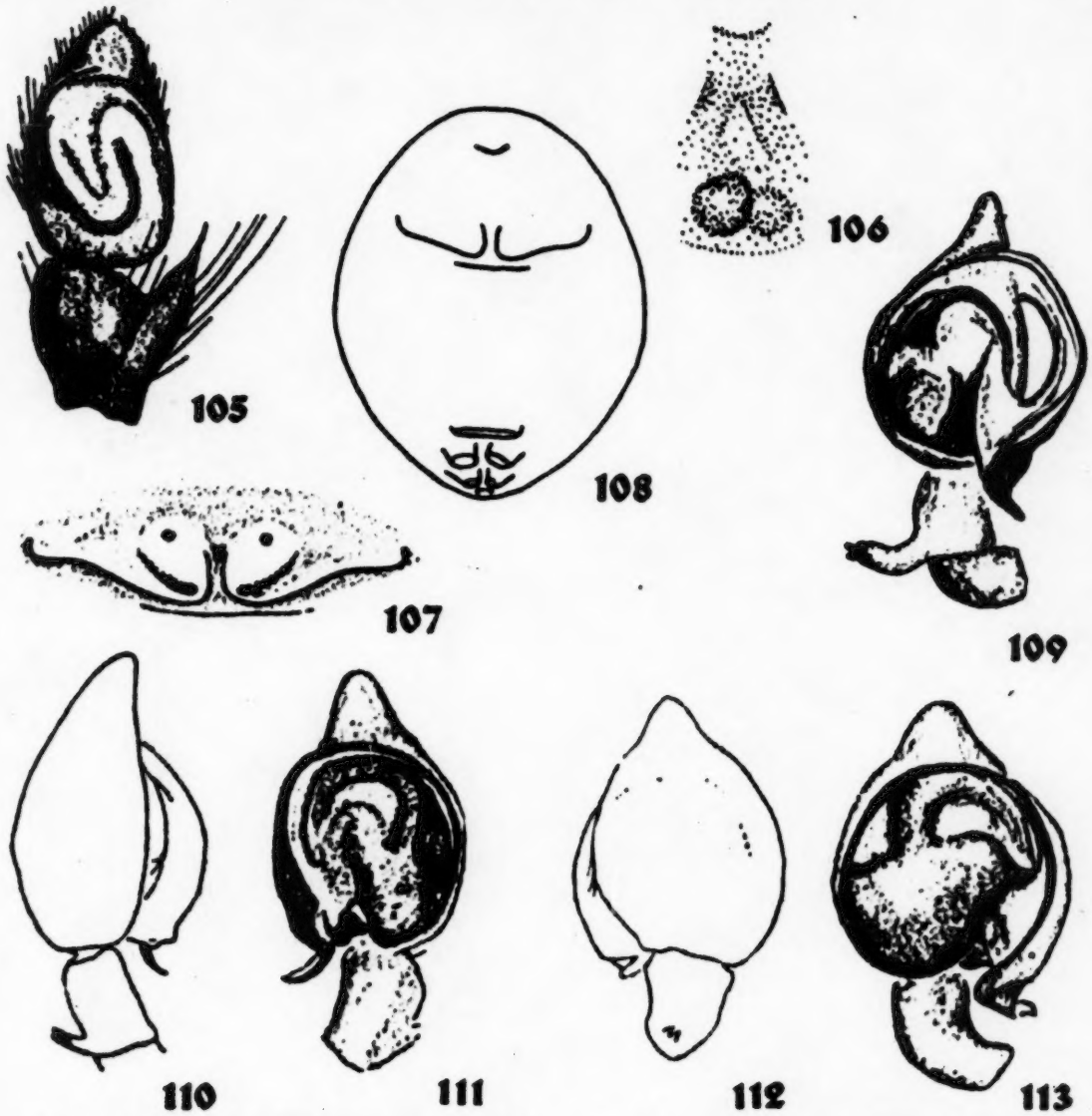
D. annulipes Blackwall, 1846.—Fairly common.

D. bicornis Emerton, 1915.—POLK Co.: St. Croix Falls (Gertsch).

D. bostoniensis Emerton, 1888.—BROWN Co.: Green Bay; KEWAUNEE Co.: Algoma.

D. coloradensis Chamberlin, 1919, figs. 107, 108, 109. Chamberlin, R. V. 1919, Ann. Ent. Soc. Am. 12:241, figs. 6, 8.—Fairly common.

D. cruciata Emerton, 1888.—DANE Co.: Madison; PIERCE Co.: Maiden Rock; SAW-



Figs. 105-113.—105. *Sitticus cursor* Barrows, palp, ventral view (Ohio); 106. *Sitticus cursor* Barrows, epigynum; 107. *Dictyna coloradensis* Chamberlin, epigynum; 108. *Dictyna coloradensis* Chamberlin, abdomen of female, ventral view; 109. *Dictynia coloradensis* Chamberlin, palp, ventral view; 110. *Dictyna alias* Chamberlin, palp, dorsal view; 111. *Dictyna alias* Chamberlin, palp, ventral view; 112. *Dictyna manitoba* Ivie, palp, dorsal view (Minn.); 113. *Dictyna manitoba* Ivie, palp, ventral view (Minn.).

YER Co.: *Lac Court Oreilles: MARQUETTE Co.: Endeavor.

D. foliacea (Hentz, 1850).—BAYFIELD Co.: Port Wing; DOUGLAS Co.: Brule; GRANT Co.: *Wyalusing; IOWA Co.: Arena; Barneveld; ONEIDA Co.: Lake Tomahawk; RICHLAND Co.: Gotham; PORTAGE Co.: Stevens Point; WALWORTH Co.: College Camp, Delavan, Lake Geneva.

D. hentzi Kaston, 1945.—CRAWFORD Co.: Prairie du Chien; DANE Co.: Madison; WALWORTH Co.: Sugar Creek.

D. longispina Emerton, 1888.—DANE Co.: Madison; TREMPEALEAU Co.: Perrot State Park.

D. manitoba Ivie, 1947, figs. 112, 113.—WALWORTH Co.: College Camp.

D. minuta Emerton, 1888.—ADAMS Co.: Wisconsin Dells; BAYFIELD Co.: *Bayfield; CLARK Co.: *Colby; CRAWFORD Co.: Prairie du Chien; DANE Co.: *Madison; LA CROSSE Co.: *La Crosse; SAWYER Co.: *Lac Court Oreilles; TREMPEALEAU Co.: Perrott State Park; WALWORTH Co.: Lake Geneva.

D. sublata (Hentz, 1850).—Common.

Lathys foxii (Marx, 1891).—In forest litter. DOOR Co.: Peninsula State Park.

Scotolathys pallidus (Marx, 1891).—In forest litter. DOOR Co.: Peninsula State Park; MARATHON Co.: Rib Mountain; SAWYER Co.: Flambeau State Forest; SHAWANO Co.: Neopit.

ULOBORIDAE—Hackled-Band Orb Weavers, Cribellate Spiders

Hyptiotes cavatus (Hentz, 1847). Triangle spider.—DANE Co.: *Madison; JUNEAU Co.: Rocky Arbor Roadside Park; VILAS Co.: *Trout Lake.

Uloborus americanus Walckenaer, 1841. Featherlegged spider.—Fairly common.

AMAUROBIIDAE—Hackled Band Weavers, Cribellate Spiders

Callobius bennettii (Blackwall, 1846) (*Amaurobius bennettii* Kaston, 1948).—Under logs and stones in woods. Very common.

Titanoeca americana Emerton, 1888.—BURNETT Co.: *Siren; DANE Co.: *Madison; PORTAGE Co.: Stevens Point; ROCK Co.: *Milton; WAUSHARA Co.: *Pine River.

Walmus borealis (Emerton, 1909) (*Callioplus borealis* Kaston, 1948).—FLORENCE Co.: Tipler; MARATHON Co.: Rib Mountain, Hogarty; VILAS Co.: *Trout Lake.

ERRONEOUS RECORDS

Cybaeus reticulatus tius Chamberlin and Ivie, 1932. Chamberlin, R. V. and W. Ivie, 1932, Bull. Univ. Utah 23(2) Biol. Ser. 2(1):19.—Recorded from "Longmire, Wisconsin." According to Mr. W. Ivie (pers. comm.) this is a misprint and should read Longmire, Washington.

Meta mengei (Blackwall, 1870.) *Epeira peckhamii* McCook, 1893, American Spiders 3:189, pl. 18, figs. 5-6. *Meta reticulata* var. *mengei* Wiehle, 1931 in Die Tierwelt Deutschlands, Araneidae, 23 Teil; VI p. 123, figs. 198-199. *Epeira peckhami* Levi, 1951. Am. Mus. Nov. 1501:15.—According to McCook (1893), *Epeira peckhamii* was found in Florida and Wisconsin. On examining McCook's collection at the Academy of Natural Sciences in Philadelphia, the collection proved to have two vials, one labeled *Epeira peckhamii* McCook Fla., another *Zilla peckhami* McC., Wisc. The two vials contained different species. Dr. W. J. Gertsch identified the contents of the Zilla vial as *Meta mengei* (Blackwall) a spider common in Europe. Most likely this record is an error of locality since *Meta mengei* has otherwise not been found in America. The description and drawings of *Epeira peckhamii* McCook, 1893 were made from specimens of *Meta mengei* and the former name is a synonym of the latter.

SUMMARY

FAMILIES	GENERA	SPECIES
Atypidae	1	1
Dysderidae	1	1
Scytodidae	1	1
Pholcidae	2	2
Theridiidae	19	36
Nesticidae	1	1
Linyphiidae	15	28
Micryphantidae	33	54
Epeiridae	20	40
Theridiosomatidae	1	1
Tetragnathidae	4	13
Mimetidae	2	4
Agelenidae	6	14
Hahniidae	2	3
Pisauridae	2	5
Lycosidae	8	35
Oxyopidae	1	2
Gnaphosidae	12	26
Clubionidae	7	26
Anyphaenidae	2	3
Thomisidae	10	32
Salticidae	26	46
Dictynidae	4	15
Uloboridae	2	2
Amaurobiidae	3	3
Total:	185	394

REFERENCES

ARCHER, A. F. 1950—A study of theridiid and mimetid spiders with descriptions of new genera and species. Alabama Mus. Nat. Hist. Mus. Pap. 30:1-40.

———1951—Studies in the orbweaving spiders (Argiopidae). Am. Mus. Nov. 1487:1-52, and 1502:1-34.

COMSTOCK, J. H. 1940—The spider book. Doubleday, Doran & Co. Inc. rev. and edit. by W. J. Gertsch. 729 pp.

FIELD, H. M. 1938—Spiders of Wisconsin: their classification and distribution. Thesis, Univ. of Wisconsin. 164 pp.

GERTSCH, W. J. 1949—American spiders. D. Van Nostrand Co. Inc. 285 pp.

KASTON, B. J. 1948—Spiders of Connecticut. Conn. Geol. Nat. Hist. Surv. Bull. 70:1-874.

MCCOOK, H. C. 1893—American spiders and their spinningwork. Vol. III. Published by author. 284 pp.

Mammals of Gulf Hammock, Levy County, Florida

Paul G. Pearson
University of Florida, Gainesville

The following report is that of a regional study which contributes to the knowledge of Florida mammals.* The tract known as Gulf Hammock is one of the most undisturbed forest areas in northern Florida. This area borders the Gulf of Mexico between the coastal towns of Cedar Key and Yankeetown, which are shown on map 1. Investigation of the region was conducted twice monthly between June 1949, and May 1950, and during the entire summer of 1950.

The area lies at an elevation of less than 25 feet above sea level. Limestones and dolomites of Eocene form the solid bedrock which is mantled with Pleistocene deposits and organic soils. The soils are at most only a few feet in thickness and they become saturated during seasons of heavy rainfall. The entire area may occasionally be inundated.

Rainfall is unevenly distributed throughout the year, with the period from June through September being the time of heaviest precipitation, while November, April and May are the months of least precipitation. The extensive forest canopy modifies the effects of wind and temperature to a considerable degree.

The major streams in this low, slightly undulating area are the Waccasassa River and Dry Creek. The Waccasassa River has many tributaries, some of which are indicated on map 1. Intermittent drainage areas, locally known as sloughs, vary considerably in the periods they remain flooded but none is flooded continuously. They have thick deposits of organic soils and they are dominated by hydrophytic forest communities.

The streams exhibit wide variation in the amount of water carried and therefore the adjacent areas are subjected to periodic flooding and excessive drying. During periods of heavy and continued rainfall the Waccasassa channel is unable to handle the water it receives from its system and so backs up and submerges the low areas. Evidence gathered from local residents indicates that nearly the entire study area (fig. 1) was submerged after the hurricane of September 1950. During months of little or no rainfall the opposite extreme exists. Most of the surface drainage of the study area becomes stagnant and ceases to flow and the interstream areas are thoroughly dried out.

The vegetation was examined in the study area indicated on map 1. The nomenclature for the plant communities has been adapted from the works of Laessle (1942) and Swindell (1949) and in general, the stages of succession described for Welaka in Putnam County, Florida, appear to be pertinent in Gulf Hammock. The factors which appear to have the greatest effect on the vegetational associations are the depth of soils above the calcareous bedrock, the length of time the soils remain saturated or flooded, the lumbering activities, the effects of the semi-wild cattle and hogs and of native animals. The

* The assistance of Dr. H. B. Sherman, who gave generous aid in this work, is gratefully acknowledged. Permission to work in the Gulf Hammock Federal Management Area and cooperation in many ways was kindly given by Project Leader David E. Swindell, Jr. For contribution of data and for aid and companionship afield I am indebted to Dr. B. B. Leavitt and Mr. W. L. Jennings. I am grateful to Miss Lillian Arnold and Dr. A. M. Laessle for aid in the study of plant communities.

twelve plant communities in the area can be divided into three major divisions, which are the conifer forests or pine flatwoods, the hardwood forests or hammock and swamp communities, and the marsh or halophytic communities. The plant nomenclature used for trees is according to West and Arnold (1946), and for the remaining vegetation according to Small (1933), except where it conflicts with the International Code for Nomenclature.

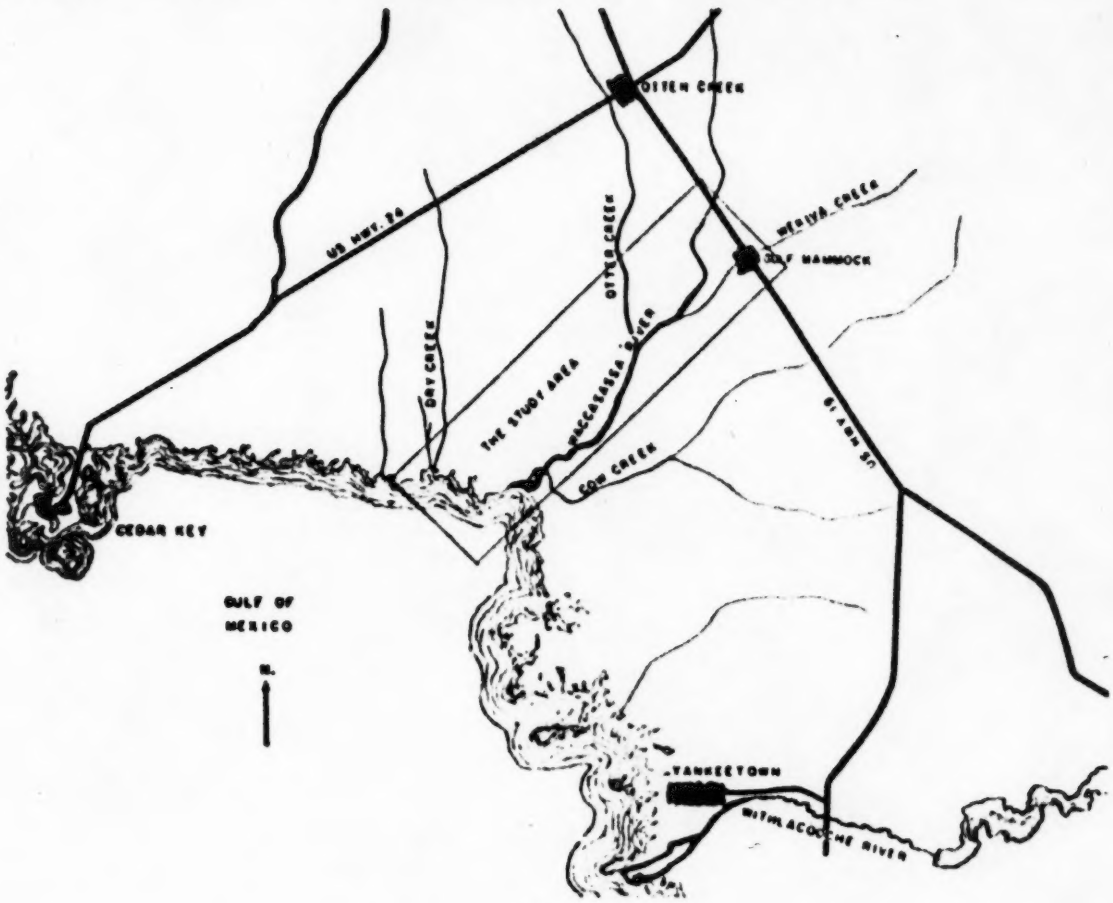


Fig. 1.—Gulf Hammock area

PLANT COMMUNITIES

Scrubby flatwoods occur at the highest elevations in the pine woods and consequently have the best drained soils. Twin live-oak (*Quercus virginiana geminata*) occurs characteristically and dominantly here. Other shrubs, commonly found in this association, are staggerbush (*Xolisma ferruginea*), scrub-oak (*Quercus myrtifolia*), running-oak (*Quercus pumila*), Chapman's oak (*Quercus chapmanii*), saw palmetto (*Serenoa repens*), wild olive (*Osmanthus americanus*), and a blueberry (*Vaccinium myrsinites*). The herbaceous vegetation includes wire grass (*Aristida stricta*), deer tongue (*Trilisa odoratissima*), and sun rose (*Crocanthemum corymbosum*).

Long leaf pine flatwoods occur on the higher and better drained soils, although they are more poorly drained than the scrubby flatwoods. Long leaf pine (*Pinus palustris*) is dominant in the arboreal layer, and a dense, low shrub vegetation blankets the floor of the association in an homogeneous mixture. Dominant shrubs are saw palmetto, gallberry (*Ilex glabra*), dwarf live-oak (*Quercus minima*), and running-oak; while staggerbush, tar flower (*Be-*

faria racemosa), and a blueberry are common. The herbaceous vegetation is predominantly wire grass, road grass (*Eleocharis baldwinii*), and *Aristida spiciformis*. Deer tongue (*Trilisa odoratissima* and *T. paniculata*), black root (*Pterocaulon undulatum*), Indian reed (*Sorghastrum secundum*), and broom sedges (*Andropogon* spp.) are common.

The *slash pine flatwoods* are found in the major portion of the pine woods. This community differs edaphically from the ones mentioned above by occurring in the low and poorly drained areas, and vegetationally by having the shrubs clustered in small patches or "tussocks" of lush growth which are surrounded by more extensive areas dominated by herbaceous vegetation. The arboreal vegetation is dominated by slash pine (*Pinus ellioti*) with occasional cabbage palms (*Sabal palmetto*). Shrubs common in this association are saw palmetto, gallberry, dwarf sumac (*Rhus copallina*), and wax myrtle (*Myrica cerifera*). Dominant herbaceous vegetation includes hard-head (*Xyris elliottii*), Queen's Delights (*Stillingia* sp.) and broom sedges (*Andropogon capillipes* and *A. longiberbis*). Common herbs in this association are St. John's wort (*Hypericum aspalathoides*), wire grass, *Sabbatia dodecandra, Lobelia glandulosa* and *Erigeron vernus*.

The small *cypress ponds* which are found in shallow depressions of the flatwoods usually contain water, at least, in their deeper parts, for all but short periods of the year. Dominating these areas are pond cypress (*Taxodium ascendens*) and bald cypress (*T. distichum*). Common trees are black gum (*Nyssa sylvatica biflora*), dahoon (*Ilex cassine*) and willow (*Salix longipes*). In the outer portions of the ponds slash pine is characteristic. Shrubs are sparse except on "tussocks" of higher ground within the pond and on these wild rose (*Rosa* sp.), buttonbush (*Cephalanthus occidentalis*) and Virginia willow (*Itea virginica*) are typical.

Marginal thickets are ecotones of variable width occurring between flatwoods and other plant communities. They generally occupy moist soils and are characterized by a dense, lush growth of shrubs, and the mixture of plant species typically found in the adjacent plant communities. Trees that often occur here are sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), laurel oak (*Quercus laurifolia*), black gum, and slash pine. Shrubs that occur in these thickets are wax myrtle, fetterbush, saw palmetto, staggerbush and gallberry. Marginal thickets also occur at the edge of areas that have been extensively cleared of vegetation within the hammock proper. In these associations cabbage palm and loblolly pine (*Pinus taeda*) occasionally occur.

In this area, the best drained hammocks are the *mesic hammocks* which occur on the "elongated ridges" of Pleistocene deposits, and this community is recognized as the climax hardwood forest of the area. These hammocks are characterized by an association of Florida maple (*Acer floridanum*), cow oak (*Quercus prinus*), magnolia (*Magnolia grandiflora*), ironwood (*Carpinus caroliniana*), hop hornbeam (*Ostrya virginiana*), and basswood (*Tilia floridana*). Other trees commonly found in this association are live oak (*Quercus virginiana*), Laurel oak, American holly (*Ilex opaca*), pignut hickory (*Carya glabra megacarpa*), redbay (*Persea borbonia*) and *Aralia spinosa*. Characteristically found in the shrub layer are yaupon (*Ilex vomitoria*), French mulberry (*Callicarpa americana*), arrowwood (*Viburnum semitomentosum*), sparkle-

berry (*Vaccinium arboreum*), saw palmetto and strawberry bush (*Euonymus americanus*). Prominent vines are poison ivy (*Rhus radicans*), pepper vine (*Ampelopsis arborea*), scuppernong (*Vitis rotundifolia*), Smilax sp., cross-vine (*Bignonia crucigera*) and Virginia creeper (*Parthenocissus quinquefolia*). Found in the sparse herbaceous layer are woods grass (*Oplismenus setarius*), elephant foot (*Elephantopus tomentosus*), partridge berry (*Mitchella repens*), *Melothria crassifolia, Panicum joorii* and wild yam (*Dioscorea* sp.).

Hydric hammocks occur in low areas that have moist, deep organic soils that may be temporarily flooded. This community is ecotonal in nature since the arboreal plant species also occur in climax mesic hammock and in swamp. Swamps occur at lower elevations and are more permanently flooded than hydric hammocks. However, hydric hammocks can usually be distinguished from swamps by the herbaceous complex, for the density and number of species of herbs is much less in the swamp than in the hydric hammock. Occurring typically in hydric hammock are Florida elm (*Ulmus floridana*), laurel oak, sweetgum, hackberry (*Celtis laevigata*), cabbage palm and ironwood. Trees of common occurrence are water hickory (*Carya aquatica*), shumard oak (*Quercus shumardi*), swamp redbay (*Persea palustris*) and ash (*Fraxinus* sp.). Shrubs present in the hydric hammock are wax myrtle, parsley hawthorn (*Crataegus marshallii*), shining hawthorn (*Crataegus aestivalis*) and tough dogwood (*Cornus stricta*). Herbaceous vegetation includes ironweed (*Vernonia* sp.), mistflower (*Eupatorium coelestinum*), *Hyptis radiata, Justicia* sp., *Centella repanda, Elytraria carolinensis* and *Pluchea longifolia.*

In the *swamp* prominent trees are black gum, bald cypress, ash, sweet gum, cabbage palm, dahoon, red maple (*Acer rubrum*) and sweet bay (*Magnolia virginiana*). Of common occurrence are water locust (*Gleditsia aquatica*), swamp red bay, water hickory and Florida elm. Shrubs typically found are Virginia willow, parsley hawthorn, buttonbush, bigleaf snowbell (*Styrax grandifolia*), indigobush (*Amorpha* sp.) and buckeye (*Aesculus pavia*). The herbaceous vegetation includes lizard's tail (*Saururus cernuus*), smartweed (*Polygonum* sp.), milkweed (*Asclepias* sp.), *Justicia* sp., blue flags (*Iris* sp.) and mist flower.

The *coastal hammock* is an hydrophytic association occupying a belt of variable width along the landward side of the salt marsh. The coastal hammock has an elevation slightly higher than the salt marsh, but is flooded by sea water at irregular intervals. Fires burn from the salt marsh into the edge of the hammock on occasions, but they fail to penetrate the hammock to any great extent. The arboreal vegetation is dominated by cabbage palm, red cedar (*Juniperus silicola*), and live oak, while Florida elm and hackberry occur frequently. The arboreal vegetation nearly excludes other plants, but young cabbage palm and cedar occasionally form a dense lower layer. St. Augustine grass (*Stenotaphrum secundatum*) occurs as a well sodded, lawn-like component of the association. Carpet grass (*Axonopus* sp.), elephant foot, and woods grass occur abundantly in some areas.

The *coastal savannah* is a halophytic community that is of variable width between the salt marsh and hammock communities. Arboreal cover is limited to an occasional cabbage palm, but shrubs may be represented by marsh elder (*Iva frutescens*), Christmas berry (*Lycium carolinianum*) and groundsel tree (*Baccharis halimifolia*). Prominent amongst the numerous herbs are glasswort (*Salicornia perennis*) and (*S. bigelovii*), saltwort (*Batis maritima*), salt

grasses (*Distichlis spicata*) and (*Spartina patens*), sea ox-eye (*Borrichia frutescens*), sea blite (*Suaèda linearis*) and sea lavender (*Limonium carolianum*).

The *salt marsh* varies from one to three miles in width. It borders the Gulf of Mexico and is dominated by black rush (*Juncus roemerianus*) almost to the exclusion of other vegetation. The soils are saturated and the spring high tides cover much of the marsh. It is netted with a vast system of tidal creeks, and marsh ponds are scattered throughout.

Ruderal communities at three abandoned farms on the area are abandoned fields that are invaded by wax myrtle, sweet gum, and persimmon (*Diospyros virginiana*). Bladder pod (*Glottidium vesicarium*) is abundant and dog fennel (*Eupatorium* sp.), rag weed (*Ambrosia* sp.), carpet grasses (*Axonopus* spp.), *Panicum* spp., *Paspalum* spp., and broom sedges (*Andropogon* spp.) occur frequently.

METHODS

The major portion of the data presented was collected by use of traps, and the greater portion of the trapping was done with the Sherman live trap which measures 2 x 2½ x 6½ inches. Collapsible wire traps made by the National Live Trap Company were also used. These were of two sizes, 6 x 6 x 19 and 9 x 9 x 27 inches. Moles were trapped with the "out-o-sight" trap made by the American Trap Company of America. Oneida jump traps were used in the steel trapping operations.

Since the study area was within the Gulf Hammock Federal Management Area where guns are generally prohibited, hand collecting was especially important in the collection of bats. Guns were rarely employed.

The Sherman traps were set at intervals of 25 to 100 feet, usually at 50 feet. The major portion of the small mammal trapping was done with the traps set on the ground surface, but traps were also set inside hollow logs, inside rotten stumps, on floating logs, on high stumps, and in underground burrows. Oatmeal, and yellow and white cornmeal were used as baits. Some of the small mammals caught were killed and removed, but others were marked and released to study population problems. The interpretation of these population data was included in another paper (Pearson, 1953).

The mammalian fauna of the various plant communities was examined by trapping in 35 study plots distributed throughout the area. Ten of these 35 plots were in flatwoods communities, 20 were within the hammock, and five were in the halophytic communities. The number of Sherman trap nights concentrated in each of the plant communities and the number of small mammals caught in them are given in table 1.

Data on specimens listed below are recorded respectively as total length, tail length, length of hind foot, ear length from crown, and weight. Specimens were usually measured before *rigor mortis* and the resulting measurements are given in millimeters and grams. Catalogue numbers refer to specimens prepared and in the collection of the author (Pe), or the collection of the Department of Biology, University of Florida (DB). Measurements not preceded by a catalogue number are those of animals that were not preserved.

ACCOUNTS OF SPECIES

Didelphis virginiana pigra Bangs. Florida Opossum.—The opossum was recorded in the hammock communities and in slash pine flatwoods, but the greatest activity was ob-

TABLE 1.—Summary of small mammal trapping

	Long leaf pine flatwoods	Slash pine flatwoods	Scrubby flatwoods	Cypress ponds	Marginal thicket	Mesic hammock	Hydric hammock	Coastal hammock	Swamp	Coastal savannah	Salt marsh	Ruderal	Totals
Sherman trap-nights	150	120	209	104	694	2342	626	105	82	80	147	195	4854
Cryptotis floridanus													
individuals											1		1
Peromyscus gossypinus													
total captures				2	74	335	131	7	14		9	2	574
individuals				1	49	141	52	7	8		9	2	269
Peromyscus nuttalli													
total captures					3	91							94
individuals					3	20							23
Oryzomys palustris													
individuals											6		6
Sigmodon hispidus													
total captures	18	3	14		58	5				1			99
individuals	18	3	14		54	4				1			94

served around the village of Gulf Hammock. They were trapped with apple, prunes, peanuts, corn, and sardines used as bait.

Jennings, while trapping for gray squirrels, took six opossums which he marked and released. A male taken December 22, 1949, was retaken 21 days later 300 yards from the point of release. One opossum taken January 28, 1950, was retaken two months later at the original point of capture.

One opossum regurgitated a leopard frog when it was released from a trap.

Measurements of six specimens are: ♂ 650 295 63 39 1,240—12-17-49; Pe 184 ♂ 500 222 47 37 400—7-14-50; ♂ 437 202 41 31 252—6-24-50; ♀ 658 288 63 32 1,615—1-7-50; ♀ 610 285 60 34 700—8-12-50; ♀ 435 210 43 37 282—9-19-49.

Scalopus aquaticus. Florida mole.—The distribution of Florida moles needs extensive study, and the material should be examined using statistical tools to present a lucid picture. Recently Schwartz (1952) listed three males of *Scalopus aquaticus parvus* from the Gulf Hammock region. These three and the five males from this study have been examined and are tentatively denoted as intergrades between *parvus* and *australis.* These Levy County specimens were compared with eight topotype *australis* males from the private collection of H. B. Sherman. Two standard errors of each mean were plotted for characters studied and these parameters overlapped each other. This is usually considered to indicate the lack of significant difference between means of two populations. The best character to separate the Levy County specimens from topotype *australis* is the greatest skull length. Jackson (1915) gives the average and extreme measurements of three *parvus* males from Port Tampa City as greatest skull length: 30.6 (30.2-31.2). As seen below the measurements of this character for the Levy county moles is intermediate between the Tampa *parvus* males and the *australis* males. In regard to color, Jackson (1915) says the color of *parvus* is similar to that of *australis.* Since specimens from each locality are quite variable, diagnosis was not based on color. The measurements, respectively, are the mean, the standard deviation, and the range first of Levy County specimens and secondly Alachua County specimens. Total length: 140.7, 5.0, 132-149; 142, 5.8, 128-149. Tail: 22.6, 2.6, 19-28; 23.6, 3.1, 20-30. Foot: 17.5, .9, 16-19; 17.3, .4, 16-18. Skull, greatest length: 31.2, .61, 30.2-31.9; 31.8, .3, 31.3-32.3. Palatal length: 12.95, .37, 12.2-13.3; 13.0, .57, 12.2-13.9. Mastoid breadth: 16.3, .4, 15.6-16.9; 16.65, .33, 16.1-17.4. Interorbital width: 7.14, .1, 7.0-7.4; 7.2, .22, 6.8-7.5

Evidence of mole activity was regularly observed in all but the flooded and halophytic communities. Measurements of five moles are as follows: Pe 168 ♂ 146 22 18 46—5-2-50; Pe 178 ♂ 140 21 17 43—6-14-50; Pe 188 ♂ 148 21 18 47—8-9-50; Pe 190 ♂ 157* 25 19 45—8-14-50; Pe 191 ♂ 138 19 17 44—8-15-50.

Cryptotis floridana (Merriam). Florida Short-tailed Shrew.—Trapping results in the study area indicate that shrews are quite rare. One specimen was trapped February 12, 1950, on a creek bank in the salt marsh. It was pregnant and its three embryos measured 14, 15, 15 mm. in crown-rump length. The adult female, Pe 146, measured 85 24 12 5 mm.

Myotis austroriparius (Rhoads). Southeastern Little Brown Bat.—This bat is common throughout the hammock area and is usually observed over ponds and clearings within the hammock, or during the day it may be found under the highway and railroad bridges near the area. Two male specimens, Pe 187 and Pe 185, taken July 26, 1950, and July 12, 1950, measured 87 40 9 10 mm. and 93 54 10 10.5 mm., respectively.

Lasiurus seminolus (Rhoads). Seminole Bat.—Seminole bats were observed only in flatwoods communities. Specimens were shot July 21, 1949, and August 21, 1949. Testes measurements of the latter specimen were 8 x 3 mm. with the epididymis dissected away, while the specimen measured 104 46 9.

Corynorhinus macrotis (LeConte). LeConte Lump-nosed Bat.—This species, seldom recorded in Florida, was observed July 25, 1950, in a deserted shack near the mouth of Wekiva Creek. It was hanging on the rough cypress walls of the dark, damp cabin, but it was immediately active when approached and several attempts to swat it failed. A local resident reported four "long eared" bats in his damp boat house the first week in July and another resident killed a similar bat in a closet in his cabin.

---

* Measured after *Rigor mortis* had set in.

A *Corynorhinus* was shot by Jennings in a deserted camp house. However, the bat was only stunned by the shot, and when it was picked up the ears were rolled in a fashion resembling the coil in ram's horns. Swindell collected three specimens in a deserted camp house near US Highway No. 19 several miles south of Gulf Hammock, September 22, 1950, and the testes of one specimen measured 10 x 4.5 mm. Swindell collected another bat from this cabin as late as October 13, 1951, whose testes measured 6 x 4 mm. Measurements of these five specimens are: Pe 189 ♂ 96 47 13 39 7—8-12-50; Pe 196 ♂ 108 46 12 29 ..—9-22-50; Pe 197 ♀ 111 47 12 28 ..—9-22-50; Pe 198 ♀ 106 50 12 28 ..—9-22-50; DB 928 ♂ 102 49 11 28 7.8—10-13-50.

Ursus floridanus (Merriam). Florida Black Bear.—Various reports by residents of the Gulf Hammock area indicate that the bear has been absent, or nearly so, for the past decade. Since the natives regard the bear as a destroyer of property, it has been hunted and killed. However, in May 1949, a bear destroyed some bee hives, and a pack of hounds was put to chase. The bear, weighing 128 pounds, was shot the following day.

Damage to a stand of bee hives located in slash pine flatwoods south of the village of Gulf Hammock was reported several times late in September 1949. Another hive was destroyed on September 27, 1949. To eat the honey the bear lifted the hive away from the stand possibly one section at a time, and deftly removed the comb and honey from the frames. Although the frames were scattered over several hundred feet, the majority of them were not damaged and could be used again. A bear destroyed 15 of 16 hives near Yankeetown in November 1949.

Procyon lotor elucus Bangs. Raccoon.—Raccoons were most abundant in the hydric situations although they were recorded in all plant communities. In 1949, and the early months of 1950, the raccoon population was at a peak, for the natives of the area reported that more raccoons were present than in many years and they believed the cause to be the lack of trapping due to low prices of fur. Evidence of raccoons was noted less often beginning in April 1950, even though no commercial trapping had been done during the winter. The raccoons killed in April were heavily infested with ticks and were thin and in poor condition. Three wildlife officers and four biologists who worked in the area observed only five raccoons from July 1 to August 31, 1950.

During 1949 raccoon tracks were so abundant in the salt marshes that they wore "highways" in the soft mud. From June to September 1950, tracks were seen only occasionally and were not abundant. Therefore it seems that a peak in the raccoon population was reached in the winter of 1949-1950, and that during the spring and summer of 1950, the population was greatly reduced.

Data on seven specimens collected in Gulf Hammock are: ♂ 570 180 108 50 2,034—9-19-49; Pe 169 ♂ 785 280 118 45 3,500—4-2-50; ♂ 730 300 110 45 5,500—4-5-50; ♂ 800 260 120 44 .....—11-4-49; Pe 184 ♀ 510 160 90 46 .....—3-28-49; Pe 170 ♀ 740 240 117 .... 3,600—4-15-50; ♀ 700 220 115 45 .....—2-6-50.

Mustela frenata peninsulae (Rhoads). Florida Weasel.—The only record from this locality was a highway casualty, which Jennings picked up on US Highway No. 19, 0.7 mile north of the village of Gulf Hammock on January 21, 1950. The body of this male specimen was crushed but the following measurements were made: — 140 49 16.

Mustela vison lutensis (Bangs). Florida Mink.—Mink are quite common in the salt marshes of the area. One professional trapper told the author in February 1950, that this past season had been a poor mink year because of the weather conditions. His instructions for trapping mink indicated that he trapped on the coldest days of the year when a northeast wind had blown most of the water out of the salt marshes. He said the best trapsite was made from a hollow cabbage palm log. Fish, oysters, or other meat were placed inside the log, one end was blocked and a steel trap was set in the other entrance. He believed that under proper conditions mink were as easily trapped "as rats."

Dr. Sherman obtained three skeletons from a mink trapper January 15, 1949, and the two male and one female skeletons, DB no. 313, 314, and 312, respectively, measured: 520 170 60; 525 145 52; and 480 145 52.

Lutra canadensis vaga (Bangs). Florida Otter.—Otter are quite abundant in this area and they have been frequently observed in the larger streams of the area. A local resident, Mr. McMillan, who rides the woods daily and sees many otter, observes more in the larger streams, i.e. Otter Creek, than he does in the hammock ponds, sloughs, or salt

marshes. He reported seeing a living otter that had an open wound several inches in diameter on top of its head.

A male specimen, DB No. 668, was picked up on US Highway No. 24 two miles northeast of the town of Otter Creek by Steve Fickett and it measured 1,110 43 135 30.

Mephitis mephitis elongata (Bangs). Florida Skunk.—The skunk is not abundant in the area and is rarely observed. Two were seen along a dirt road the night of February 10, 1950, and were apparently feeding. A skunk skeleton was found in flatwoods early in June 1950.

Urocyon cinereoargenteus floridanus Rhoads. Gray Fox.—Foxes are rare in the hammock area, although they are abundant about six miles east in the sand hills. Jennings saw a fox on a flatwoods "island" within the hardwood forest on March 4, 1950. However, local residents report that their hounds will trail foxes in other areas but on no occasion have their hounds given chase to one in the hammock of the study area.

Felis concolor coryi Bangs. Florida Panther.—Panthers do not occur abundantly in the Gulf Hammock area but they have been reported frequently from widely separated parts of the region. In March 1948, Swindell found tracks of a panther, measuring three and one-half inches in diameter, about one mile west of US Highway No. 19, south of the town of Gulf Hammock. Jennings found panther tracks which measured three inches in diameter, near a swamp east of Cedar Key on February 7, 1950. Billy Patterson, a local resident, reports that panthers have occurred around his home in Gulf Hammock and in coastal hammock on the area in the last several years.

Lynx rufus floridanus (Rafinesque). Florida Wildcat.—The wildcat, abundant in the Gulf Hammock area, was recorded in all plant communities. One native of the area, Mr. Carl Jones, has killed 88 wildcats in the last four years. He hunts by using hounds to trail, catch, and kill wildcats.

The wildcat in its attempt to "lose" the dogs usually does not maintain a fast pace, but rather depends upon its skill at setting difficult trails for the dogs to follow. About 6:30 AM September 25, 1949, a wildcat track was "struck" about six miles east of the town of Gulf Hammock, and within ten minutes the dogs had "jumped" the cat. A chase through the shrubs of the long leaf pine community followed. The race took place within 100 yards of the hunting party, and the tactics used by the cat to elude the dogs were observed.

This wildcat ran with a slow, precise, almost dainty stride past us in a fire lane ten feet away. It then made a ninety-degree turn and ran through the shrubs to a marginal thicket 500 feet away. When the dogs had nearly reached the thicket the cat retraced its path toward us, moving parallel to its entrance path. The cat then proceeded to turn and circle in several directions and to completely confuse the trails. The cat always entered a marginal thicket, a gallberry thicket, or a palmetto patch and lay down. When the dogs were close it arose and nearly retraced its path out of the thicket. It was found normal for the wildcat to walk along a log, turn around, and retrace its course and jump to another object. This made it difficult for the dogs to follow the trail.

A female wildcat caught April 30, 1950, had one well-developed embryo in each horn of the uterus. Measurement of one embryo *in utero* was 35 mm. The crown-rump measurement of the other embryo after removal was 12 mm.

Measurements of 14 adult wildcats are as follows: DB 410 ♀ 790 130 165 55 .....—2-27-49; DB 713 ♀ 870 154 173 60 8,500—5-21-50; ♀ 860 140 160 .... 7,000—4-30-50; Pe 183 ♀ 810 145 160 53 8,568—7-22-50; ♀ 660 127 127 57 .....—8-1-48; DB 703 ♂ 908 170 180 59 6,500—5-8-50; ♂ 838 153 159 51 .....—7-27-48; ♂ 1016 203 178 64 14,496—8-22-48; ♂ 1016 203 186 63 14,684 —9-12-48; ♂ 800 165 140 57 7,022—1-10-49; Pe 132 ♂ 865 155 170 55 .....—7-10-49; Pe 133 ♂ 830 154 185 58 8,500—7-31-49; Pe 167 ♂ 900 165 200 58 .....—9-25-49.

Sciurus carolinensis carolinensis Gmelin. Gray Squirrel.—The gray squirrel was abundant in the hammock communities of the study area. However, since Jennings was carrying on a study of this squirrel, little effort was made on my part to study them. Two specimens were collected, one of which was a lactating female. This animal, Pe 106, was killed June 19, 1949, and it measured 411 190 58 19 438 grams, while a young male, Pe 105, killed June 2, 1949, measured 350 165 55 19.

Sciurus niger niger Linnaeus. Southern Fox Squirrel.—Fox squirrels were observed

frequently in all flatwoods communities. Pine mast cuttings were observed under long leaf pines August 7, 1950, and under slash pines on August 17, 1950. Measurements of four specimens are: ♂ 600 280 85 21 1,108—9-27-49; Pe 134 ♀ 590 270 83 18 .....—8-22-49; Pe 192 ♀ 560 270 85 16 788—6-16-50; ♀ 605 295 86 ....—12-17-49.

Glaucomys volans querceti (Bangs). Florida Flying Squirrel.—A single specimen was collected August 20, 1949, from a pine tree, which lacked nesting material, on the rim of a cypress pond. The uterus contained three placental scars and the specimen measured 217 93 28 13. A local resident discovered a rat snake (*Elaphe obsoleta williamsi*) swallowing a flying squirrel near the village of Gulf Hammock. The squirrel was rescued and allowed to escape into the brush.

Peromyscus gossypinus gossypinus (LeConte). Cotton Mouse.—The cotton mouse is the most abundant mammal in Gulf Hammock, occurring in modal numbers in hammock communities. Measurements were made of 72 individuals, of which 25 are in the author's collection. Statistical parameters of the series are given below. Osgood (1909) recorded two cotton mice, subspecies *palmarius*, from Gulf Hammock. A major subspecific character defining the forms concerned here is that the foot of *palmarius* measures from 20 to 22 mm., while the foot of typical *gossypinus* measures from 22 to 26 mm. This large series collected in Gulf Hammock is designated as typical *gossypinus*, since the mean foot measurement was 23.0 mm. with the observed range being from 22 to 25 mm.

	N.	MEAN	STANDARD DEVIATION	RANGE
Body length	72	175.6 ± 1.2	9.9 ± .8	155-200
Tail length	72	74.5 ± .6	5.1 ± .4	64-90
Foot length	71	23.0 ± .1	.6 ± .1	22-25
Ear from crown	72	14.5 ± .1	1.1 ± .1	12-16
Weight	72	26.2 ± .5	4.3 ± .4	17-35

Since most of the field work was concentrated in plots where it was not desired to disturb the nesting and resident populations, little data were collected on nests. However, released cotton mice were followed and the types of nest sites found were rotten hardwood logs, bases of trees, cabbage palm logs and stumps. In one mesic hammock eight cabbage palm logs containing nesting material attributed to cotton mice were examined November 11, 1949. Five of these nests contained caches of partially eaten live oak and laurel oak acorns. Two nests in palm logs in coastal hammock contained no young and no stored food on April 15, 1950.

Ticks, red bugs, and fly larvae heavily parasitize cotton mice in the area. Thirty-three records of fly larvae (Cuterebridae) in cotton mice were obtained and of these, all but one were found in the genital region. The latter larva was imbedded on the lateral side of the lumbar region. In 29 instances but one larva was found per mouse, while on three occasions two larvae were imbedded in each mouse. These larvae probably parasitize cotton mice in all months of the year although they seem to be more abundant in the summer. The parasitism was observed in all months except February and March, but almost half of the observations (14 of 33) were made in June.

Seven cotton mice parasitized by fly larvae, were released and when later retaken were observed to have suffered little or no ill effects. One adult male carried a large larva on May 7, 1950, and a very small larva was observed June 15 and then again on June 30, 1950. On July 1, when this animal was retaken again, the larva had emerged since the previous day, and the mouse was dead in the trap. I do not believe that conditions were such that trap exposure alone killed this mouse and it appears that the larva contributed to the mouse's death.

The swimming and climbing abilities of cotton mice were observed on several occasions. Mice swam away from the author when they were released on "tussocks" surrounded by water, the longest distance observed being 20 feet. One mouse climbed 25 feet up a tree and disappeared into a hole in the trunk. Another mouse climbed an ironwood tree to a height of 15 feet, proceeded to the extremity of a branch extending away from the observer, jumped to the ground, and escaped into a hollow log.

Numerous records of breeding activity were obtained in the fall and winter months. Criteria used to determine breeding conditions were the size and position of the testes, the presence of embryos, and the condition of the mammary glands. Only two records of preg-

nancy were obtained in the months of May through August 1950. One specimen taken June 25, 1950, contained three embryos. One adult female was observed while carrying her young from a nest on August 6, 1949. Pournelle (1950) likewise found only one pregnant female in June, July, and August out of a total of 113 adult females taken at Welaka and Gainesville, Florida. During this summer period he found the epididymides of adult males lacking in mature spermatozoa. Of three males from Gulf Hammock which I examined for spermatozoa on July 31, 1950, and of four males likewise examined on August 31, 1950, all had motile spermatozoa.

Peromyscus nuttalli aureolus (Audubon and Bachman). Golden Mouse.—In Gulf Hammock golden mice are found most abundantly in a habitat with a dense, luxurious growth of shrubs and small trees or low hanging arboreal vegetation. They were trapped in dense marginal thickets and in mesic hammocks with extensive shrub growth. The area with the greatest amount of golden mouse activity had a dense shrub layer and a sparse herbaceous vegetation. Among the shrubs were saw palmetto, wax myrtle, yaupon, sparkleberry, gallberry, arrowwood, French mulberry, and blackhaw.

Golden mice usually climbed the nearest bush when released, and then stopped and remained motionless in full view of the observer. Rustling of leaves seemed to frighten them more than any other noise. If they were not frightened their next action was to clean themselves. A male observed for thirty minutes after release, cleaned itself and then went from leaf to leaf covering most of an American holly bush licking the leaf surfaces, which were covered with dew. This action was observed on two other occasions, and is apparently one method used by the mouse to obtain water.

On five occasions golden mice entered rotten logs when released. One of these logs was opened and in it was found an extensive network of burrows. Three golden mice entered a hollow subterranean chamber beneath a large oak tree. On the other hand, only two arboreal nests were observed in this area of dense shrubs. One nest hung ten feet above the ground, and in this nest Spanish moss formed the outer layers while the inner layers were made from finely shredded palmetto fiber.

Golden mice did not have as many ectoparasites as did the cotton mice. Ticks were attached about the nose and ears of four mice, and red bugs were found on two individuals. Fly larvae were imbedded in the genital region of two mice.

Measurements of seven golden mice are given below: Pe 142 ♂ 151 70 16 13.5 12—1-21-50; Pe 160 ♂ 161 71 19 12 ....—2-25-50; Pe 117 ♂ 154 71 . 18 12 14—6-25-50; Pe 98 ♂ 141 65 18 12 12—6-3-49; Pe 173 ♀ 164 78 18 13 16—4-16-50; Pe 172 ♀ 158 74 19 12 ....—4-16-50; Pe 99 ♀ 151 72 17 12 13—6-3-49.

Oryzomys palustris natator Chapman. Central Florida Rice Rat.—Rice rats were trapped only in the salt marsh, and they appeared to have been relatively abundant here since 41 trap nights caught six rats on February 12, 1950. However, 29 trap nights produced no captures of any kind on August 23, 1950.

Measurements of the six specimens are: Pe 147 ♂ 247 127 32 13 47—2-12-50; Pe 148 ♂ 265 130 32 13 59—2-12-50; Pe 149 ♂ 255 131 32 12 51—2-12-50; Pe 151 ♂ 245 125 31 12 54—2-12-50; Pe 150 ♀ 242 127 31 12 37.2—2-12-50; Pe 152 .... 225 110 29 12 36 —2-12-50.

Sigmodon hispidus hispidus Say and Ord. Cotton Rat.—Cotton rats were recorded in flatwoods communities, in coastal savannah, and in habitats of succession leading from cleared land to hammock. They are most abundant in flatwoods communities, and their relative abundance is indicated by the number of trap nights needed to catch one individual which are as follows: long leaf pine flatwoods, 8.33; marginal thicket, 14; scrubby flatwoods, 14.9; slash pine flatwoods, 30; saw grass marsh, 30; and coastal savannah, 80.

The stomach of a barred owl shot September 23, 1949, contained an adult cotton rat. Three wildcat scats found in the area contained hair and skeletal fragments of cotton rats.

Cotton rats had large, scrotal testes in July, August, and October 1949, and June and July 1950. Females that were lactating and had placental scars were observed April 1, June 29, and July 25, 26, 27, 1950. Females contained embryos in October 1949, and in June, July, and August 1950. These data indicate that they breed throughout much of the year.

Litter size of the cotton rat in this area as computed from eleven pregnant females averages 3.65 individuals with extremes of two to six. Meyer and Meyer (1944) found that this race of cotton rat had litters averaging 5.6 with extremes of two to ten individuals

per litter under laboratory conditions. Svihla (1929) reports the cotton rat in the field in Louisiana had litters averaging 4.75 with extremes of three to six.

Statistics on a series of adult cotton rats, of which eight are in the author's collection, are given below.

	N.	Mean	Standard Deviation	Range
Total length	36	259.6±3.2	19.2±2.3	222-295
Tail length	36	109.3±1.4	8.2±1.	95-138
Foot length	36	31.4± .2	.9± .1	29-33
Ear from crown	36	15.4± .2	1.3± .2	13-18
Weight	33	100.0±4.9	28.3±3.5	46-145

Neotoma floridana floridana (Ord.) Florida Woodrat.—Woodrats were trapped in hydric, mesic, and coastal hammock, in swamp, and around two farms. In Gulf Hammock they occur most abundantly in the ecotone between mesic and hydric communities, and it is in the drier portions of this ecotone that the majority of nests were discovered. The life history and ecology of the Gulf Hammock wood rats have been previously discussed by Pearson (1952).

Measurements of adult wood rats are as follows: Pe 165 ♀ 352 168 37 22 160—4-15-50; Pe 166 ♀ 348 169 38 22 175—4-16-50; Pe 195 ♀ 333 155 37 25 178—4-16-50; ♀ 270 78 38 23 182—3-24-50; Pe 193 ♂ 382 172 38 25 198—8-11-50; ♂ 382 175 38 24 255—7-9-50; Pe 159 ♂ 380 180 42 23 303—2-7-50; Pe 163 ♂ 370 169 37 22 230—4-15-50; Pe 141 ♂ 365 176 39 22 183—1-21-50; Pe 164 ♂ 360 169 37 22 253—4-15-50; Pe 194 ♂ 337 130 38 24 198—8-11-50; ♂ 285 75 38 22 .....—6-12-50; ♂ 270 120 35 23 92—3-19-50; ♂ 256 60 37 24 193—2-12-50.

Sylvilagus floridanus floridanus (Allen). Florida Cottontail.—The cottontail was observed in flatwoods and hammock communities. A local resident killed a rat snake (*Elaphe obsoleta williamsi*) that measured four feet four inches, which had eaten a cottontail measusing eleven inches from tip of nose to the tip of the hind foot.

Females were taken June 19, 1949, and May 8, and June 27, 1950, which were lactating, and the latter female had five small embryos.

Measurements of five specimens are: Pe 176 ♀ 390 48 103 80 .....—5-8-50; ♀ 480 60 95 80 .....—6-19-49; Pe 182 ♀ 438 40 98 84 1,700—6-27-50; Pe 181 ♂ 402 50 90 73 1,032—6-27-50; Pe 177 ♂ 365 50 85 65 .....—6-12-50.

Sylvilagus palustris paludicola (Miller and Bangs). Florida Marsh Rabbit.—One marsh rabbit was collected in mesic hammock adjacent to the low areas along the Waccasassa River west of US Highway No. 19. This specimen, DB No. 704, was taken April 28, 1950, and was lactating but not pregnant. It measured 431 35 88 62 1,572. Natives report seeing marsh rabbits in the salt marshes, and tracks and pellets were observed by the author in these marshes.

Odocoileus virginianus (Boddaert). Virginia Deer.—The deer population in the area has been replenished several times with deer trapped in various parts of the country. It is, therefore, difficult to establish subspecific rank for these animals.

Deer occur in all plant communities and their tracks are often seen. The deer are of considerable economic importance since hunters come here from much of the state to hunt. Swindell (1949) reports on the populations and management of deer in Gulf Hammock.

Discussion and Conclusions

The data collected in this study indicate that nine of the 26 species recorded in the area probably do not limit themselves to any of the major plant communities. Wildcats, raccoons, and deer were recorded in all the plant communities; moles were recorded in all but the submerged communities. While complete data are lacking, it seems probable that bears, opossums, panthers, and skunks inhabit all the major plant communities. Flying squirrels apparently live in both hammock and flatwoods communities.

Southeastern little brown bats, gray squirrels, wood rats, golden mice, and

cotton mice occur in modal numbers in the hammock communities. The golden mice were taken most abundantly in communities with a dense shrub layer and the wood rats were trapped most abundantly in ecotones between hydric and mesic hammocks.

Seminole bats, fox squirrels, cotton rats, and cottontail rabbits occur in modal numbers in the flatwoods communities. Cotton rats occur most abundantly in long leaf pine flatwoods, while they and cottontail rabbits sometimes occur in heavily timbered or ruderal areas within the hammock communities.

A short tailed shrew, rice rats, and mink were reported from the halophytic or marsh communities, although data on these species are especially incomplete.

Otters and swamp rabbits were recorded in, or closely associated with, aquatic situations in several of the major plant communities.

Foxes apparently occur only sporadically within the study area although they are quite abundant in sand hill communities in the eastern part of Levy County. Insufficient data were collected on weasels to determine habitat preferences.

The rare LeConte lump-nosed bat was collected only in dark, damp, deserted shacks within the area, and this may offer a clue to facilitate capture of this species in other regions.

REFERENCES

JACKSON, H. H. T. 1915—A review of the American moles. N. A. Fauna, 38, U. S. Dept. Agriculture.

LAESSLE, ALBERT M. 1942—The plant communities of the Welaka area. Univ. Florida Biol. Series 4:1-143.

MEYER, BERT J. AND ROLAND K. MEYER 1944—Growth and reproduction of the cotton rat, *Sigmodon hispidus hispidus*, under laboratory conditions. Jour. Mamm. 25:107-129.

OSGOOD, WILFRED H. 1909—Revision of the mice of the American genus *Peromyscus*. N. Amer. Fauna No. 28, U. S. Dept. Agriculture.

PEARSON, PAUL G. 1952—Observations concerning the life history and ecology of the Florida wood rat, *Neotoma floridana floridana* (Ord). Jour. Mamm. 33(4):459-463.

———1953—A field study of *Peromyscus* populations in Gulf Hammock, Florida. Ecology 34(1):199-207.

POURNELLE, GEORGE H. 1950—Reproduction and early post-natal development of the cotton mouse, *Peromyscus gossypinus gossypinus*. Doctor's Dissertation, Univ. of Florida, 1-79.

SCHWARTZ, ALBERT 1952—Three new mammals from southern Florida. Jour. Mamm. 33(3):381-385.

SMALL, J. K. 1933—Manual of the southeastern flora. Published by the author, xxii pp. 1554.

SVIHLA, A. 1929—Life history notes on *Sigmodon hispidus hispidus*. Jour. Mamm. 10:352.

SWINDELL, DAVID E., JR. 1949—Plant communities and other factors affecting the deer and turkey populations in Gulf Hammock. Unpublished Master's thesis, Univ. of Florida. 1-150.

WEST, ERDMAN AND L. E. ARNOLD 1946—The native trees of Florida. Univ. Fla. Press. 1-212.

Carnivores of Yuma County, Arizona

Arthur F. Halloran and Willard E. Blanchard
U. S. Fish and Wildlife Service, Yuma, Arizona & Jackson, Wyoming

In the period November 1, 1944 to April, 1951 opportunities were presented to Halloran to procure data on carnivores in Yuma County, Arizona. During part of this period the junior author was assigned to the Kofa Game Range as an assistant, and was able to secure information on the carnivores during his time in the field, many days of which included the trapping of predatory mammals.

Many mammalogists have collected in or adjacent to Yuma County, but few have had the time to devote to the study of the carnivores. In view of this fact and because of the true Lower Sonoran conditions existing in this border county we believe it of value to record the data we have assembled with the thought that the deficiencies revealed will promote further studies both in Arizona and the adjacent desert areas at the head of the Gulf of California.

ACKNOWLEDGMENTS

The authors wish to acknowledge the help of their co-owrkers in the Fish and Wildlife Service who have helped in numerous ways in assembling information. District Agent Everett Mercer who has had a state-wide experience with carnivores over a period of many years has freely made available much data that otherwise would be difficult to obtain. Captain Mervin Smith of the Arizona Game Rangers has also contributed much from his years of experience in Yuma County.

The various mammals have been identified through the courtesy of Dr. H. H. T. Jackson, Stanley Young, and Miss Viola Schantz of the Fish and Wildlife Service, Washington, D. C., and Dr. William B. Davis, Head of the Department of Wildlife Management, Agricultural and Mechanical College of Texas, at College Station, Texas. The specimens are deposited in either the Biological Surveys Collection, S. S. National Museum, Washington, D. C., or the Texas Cooperative Wildlife Collection at College Station. The measurements of the various specimens under the species accounts are total length, length of tail, hind foot, and ear from notch.

Location.—Yuma County covers 6,391,680 acres in the extreme southwestern corner of the State of Arizona (fig. 1). The county is in the Sonoran Biotic Province (Dice, 1943) and is bounded on the north and east by four other Arizona counties, on the west by California and Mexico and on the south by the Mexican State of Sonora. The Colorado River forms the western boundary of the county.

Description of the area.—The geography of the county is dominated by the presence of the Colorado and Gila rivers which converge in the southwestern corners a few miles from the city of Yuma. Large portions of the surrounding desert lands slope gently toward the confluence of these two rivers. Because of irrigation farther to the east there is not now and has not been for years a steady flow of water in the Gila River in Yuma County.

The thousands of acres of low relief desert plains are dominated largely by creosote bush (*Larrea*) while the shallow washes or arroyos that course through them are dominated by sahuaro cactus (*Cereus gigantea*), ironwood (*Olneya tesota*), palo verde (*Cercidium* sp.), brittle brush (*Encelia farinosa*), and other xerophytes. Shreve (1942) and Nichol (1943) have well described the vegetation of both these plains and the desert mountain ranges that rise abruptly and form some of the striking topography of the region. Wilson

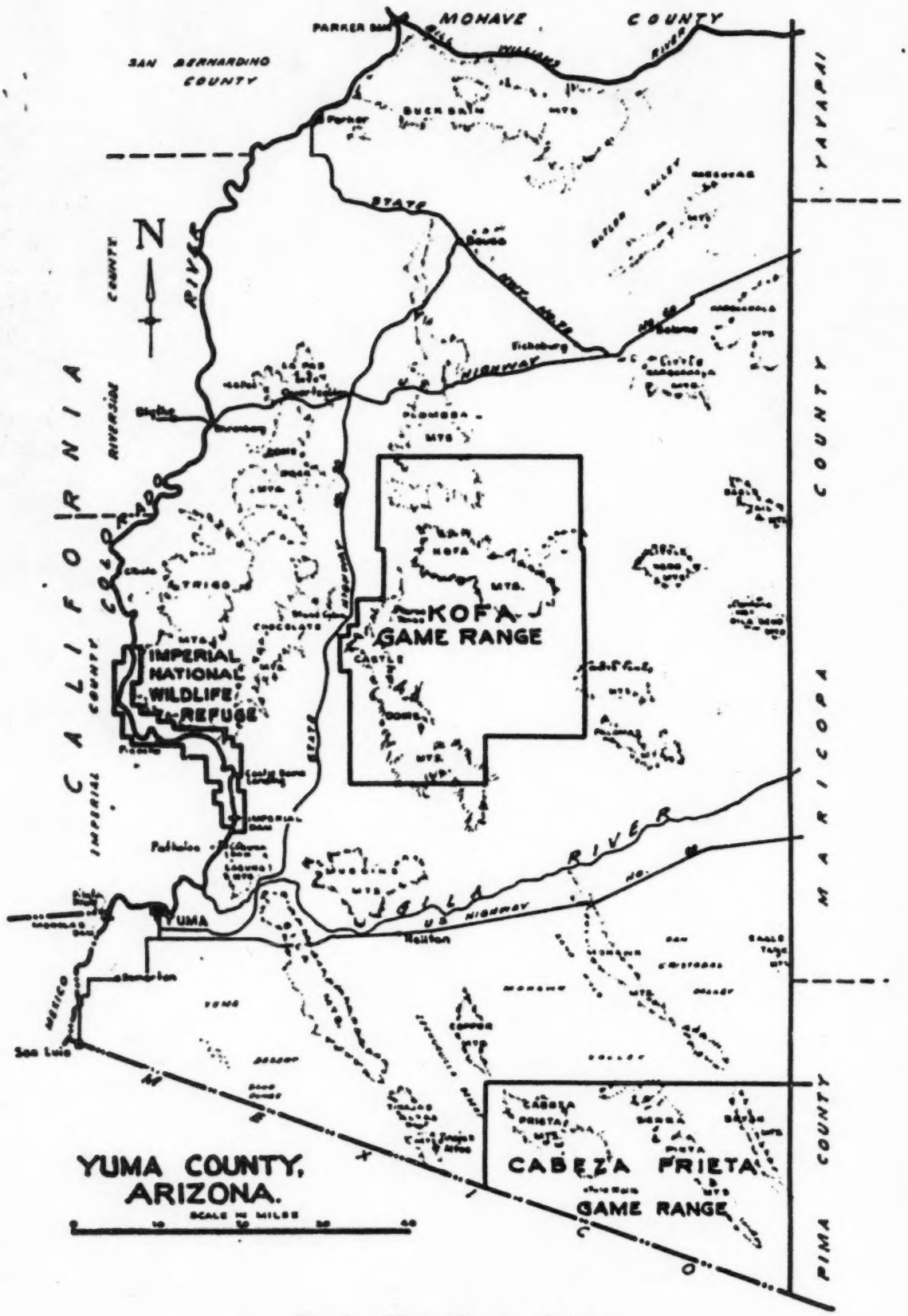


Fig. 1.—Yuma County, Arizona

(1933) in his comprehensive report of the geology and mineral deposits of southern Yuma County points out that thirty-two of these ranges or groups of mountains occupy a total of 1750 square miles (26.3%) of the southern two-thirds of the county.

In the northeastern corner the Harquahala Mountains rise to an elevation of 5,612 feet. The top of this range is an island of Upper Sonoran surrounded on all sides by the Lower Sonoran Zone which dominates the rest of the area. Signal Peak in the Kofa Mountains rises to a height of 4,828 feet above sea level and the scrub oaks (*Quercus turbinella*) and a few other plants in sheltered canyons in this range bring a suggestion of dilute Upper Sonoran. In a few canyons of this range protected from the sun by steep thick walls of rock and favored with impervious watersheds, a few palms (*Washingtonia filifera*) are to be found.

The lowest elevation in the county, 89 feet above sea level, is in the extreme southwestern corner of the county on the bank of the Colorado River just west of the hamlet of San Luis.

The climate of this low-lying desert area is characterized by the long hot summers and mild winters. The maximum temperature for the entire state as noted at a cooperative station has been recorded at both Parker and Mohawk in Yuma County at 127°F., while the all-time high for a regular U.S.D.A. Weather Bureau Station for the United States was reached in September 1950 when the thermometer touched 123°F. at Yuma. The minimum recorded temperature at Yuma is 20°F. with somewhat lower temperatures reported in lower nearby river bottom areas during the short winter season.

The average annual rainfall at Yuma is 3.41 inches, while the evaporation from a free water surface is 100.56 inches annually. A full description of these and other climatic phenomena of the State is well recorded by H. V. Smith (1945).

Hypothetical list.—We have attempted without success to find records of or local field signs of the Sonora river otter (*Lutra canadensis sonora*) in Yuma County. Grinnell, Dixon, Linsdale (1937) list the distribution of this species as, "Colorado River, on the southeastern border of the State (California)," but the two specimens they record were caught upriver from Yuma County. It is possible that this mammal exists in the county at this time within the Imperial National Wildlife Refuge where practically no legal trapping for muskrat and beaver has been allowed since 1941, but, if this is the case, it is very rare.

Two unauthenticated sight records of bears have been brought to the attention of the senior author during the past six years but, as yet, we have no basis to record that bears are now or ever have been present as indigenous residents. Most of the area is so open and suitable foods are so scarce that it is doubtful if any bears made the county their permanent home.

One unsatisfactory sight record and several sets of tracks of an animal said to be a wolf have been reported. The famous Aquila wolf (Young and Goldman, 1944) might have ranged into Yuma County, but no specific records are available to us of any wolves having been actually taken in Yuma County.

ACCOUNTS OF SPECIES

Procyon lotor pallidus Merriam.—Under date of November 1, 1948 Davis wrote, "Reference is made to your letter of January 26 and the specimen of male raccoon, your catalog No. 145. On the basis of geographic range, this is *Procyon lotor pallidus*. The specimen is not typical of *pallidus*, however, in that the face is considerably darker as are the patches behind the ears. In these respects, they are more like *mexicanus* which normally ranges west as far as the central part of Pima County. All in all, I think it best to refer the animal to *pallidus*." The specimen under discussion was taken in the cultivated area of the Yuma Valley close to the Colorado River and about 10 miles south of the city

of Yuma. A small animal, it weighed 7¼ lbs. with the following standard measurements in inches: 26¾-8½-5-2.

These Colorado desert raccoons (Goldman, 1950) are very common along the Colorado River. A large individual was seen by Halloran at 9:15 p.m. crossing a road and heading for the river at the south end of the Imperial National Wildlife Refuge on December 6, 1950. We have no sight or trapping records of raccoons from the thousands of acres of desert and mountains that lie to the east of the Colorado River bottoms.

Bassariscus astutus yumanensis Huey.—Huey (1937) described this form from Tinajas Altas, Gila Mountains (on some maps the southern end of these mountains is named Tinajas Altas Mts.) naming it the Yuma cacomistle. We found the skull of a ring-tailed cat in a small dry abandoned concrete cistern in the northern end of the Sierra Cabeza Prieta, which lies approximately 8 miles east of the Tinajas Altas Mountains (Halloran, 1947). On February 26, 1947 while camping at Horse Tanks in the northern Castle Dome Mountains, K. C. Kartchner and J. A. Kempton of the Fish and Wildlife Service noted one of these animals exploring the contents of some empty tin cans at about 9:30 p.m. Blanchard found a male "ring-tail" in one of his traps near Hidden Valley north of Horse Tanks. The writers on March 22, 1949 picked up a skull (A.F.H. no. 151) at a seep we call Sombrero Seep in the central part of the southern Castle Dome Mountains. Blanchard, in late 1943, saw four skins taken by a trapper camped at Vicksburg who had secured them a few miles to the northwest.

We surmise that these little carnivores are more common than our specimen records indicate as their tracks and signs can be found rather frequently in the dust under little ledges in the cliffs and the wind-formed caves that they inhabit.

It appears of interest to note that Grinnell (1914) did not record the ring-tailed cat on his historic trip down the Lower Colorado in 1910 although Huey (*op. cit.*, p. 359) records one from Laguna Dam (Potholes), Imperial Co., California. None of these fur-bearers was reported from Imperial County by trappers for the 1939-1940 season, but eleven were reported in the following season according to a list furnished us by the California Fish and Game Department. Burt (1938) in his paper on Sonora mammals does not include the "ring-tail" although as Huey (*op. cit.*, p. 359) states the Yuma cacomistle probably occurs in northwestern Sonora.

Spilogale gracilis arizonae Mearns.—Only one complete specimen of the little spotted skunk came to our attention. On December 28, 1947, Blanchard caught one in the Hidden Valley Hills, which lie between the northern end of the Castle Dome Mountains and the Kofe Mountains at a distance of 31 miles from the Colorado River. The individual secured contained a high percentage of white in its pelage. The skull was saved and sent to Dr. W. B. Davis at the Texas Cooperative Unit, who kindly made the identification.

The two hind feet of a spotted skunk were found in a trap at Ladder Tank (west central Castle Dome Mts.) by Blanchard. Under date of October 21, 1947 Dr. William B. Davis stated that this was the first record he had for Yuma County although there are records from Maricopa, Pinal, and Pima counties, Arizona, and Imperial County, California. Howell (1906, pp. 29, 30, pl. 1) records one from San Jose Mountains in northern Sonora.

This little skunk is rarely found in the dry desert ranges where we did most of our collecting. Possibly it is more common along the Colorado River where the cover is much heavier, but even in 1910 Grinnell (1914, p. 259) secured but one specimen. Huey (1942) however, collected two of these so-called hydrophobia skunks from rocky mountainsides at Bates Well in Pima County within the Organ Pipe Cactus National Monument.

Mephitis mephitis estor Merriam.—During several years of observation in and around the game ranges within the county the authors encountered no striped skunks on the open desert or in the dry mountain ranges. In the river bottoms and along the ditchbanks of the irrigated fields between Yuma and San Luis the tracks of these mammals can be frequently seen. It is also a rather common sight to find the remains of skunks run over on the highways adjacent to the irrigated sections of the Gila River area. Richard C. Droll caught an Arizona skunk near Castle Dome Landing in the arrowweed (*Pluchea serica*) type along the Colorado River on January 11, 1948. The skull was sent to Dr. William B. Davis who identified it on geographic grounds as *estor*. The skin, which was seen by Halloran, had a considerable amount of white in it similar to the skunk pictured by Grinnell (1914, fig. 21 facing p. 294). Burt (1938, p. 30) records no striped skunks from extreme northwestern Sonora just to the south of Yuma County in that extremely dry area between the Gulf of California and the Sonoita River.

Taxidea taxus hallorani Schantz.—The type locality of this badger is the Castle Dome Mountains, Kofa Game Range in Yuma County (Schantz, 1949). Miss Schantz records the measurements of the several specimens from Yuma County for ready reference. The heaviest badger coming to our attention weighed 9½ lbs. Two embryos were noted in a badger weighing 8½ lbs. trapped February 26, 1947 in the Castle Dome Mountains. Blanchard estimates that in the 560,000-acre Kofa Game Range there is at least one badger present on each township. Sight records by Fish and Wildlife Service personnel include a July 19, 1948 record at 7:05 a.m. at Hoodoo Well in the eastern foothills of the Kofa Mountains, as well as April and late October records of badgers traveling in gravel washes on the desert many miles from running water just before sundown. Badgers are also found in the open desert on the Cabeza Prieta Game Range at the south end of the Sierra Pinta within a mile or so of northern Sonora where similar areas dominated by creosote bush (*Larrea*) are present. On September 28, 1949 a badger weighing 8 lbs. was trapped on the shores of Martinez Lake (near Castle Dome Landing, see map).

Vulpes macrotis arsipus Elliot.—As opportunities have arisen we have sent all specimens of value of this species either to the U. S. National Museum or the Texas Cooperative Wildlife Collection. In suitable localities near sandhills or in the wide gravel washes between mountain ranges, the kit fox can still be found in Yuma County. However, in or adjacent to the desert mountain ranges the swift is scarce and is outnumbered many times by the gray fox. Under date of June 8, 1950 Stanley P. Young wrote us that two skulls procured in the Castle Dome Mountains belonged to the race *arsipus*. Benson (1938) secured two kit foxes in northwestern Sonora and after an exhaustive study of these and other specimens concluded that the kit foxes of northwestern Sonora and southwestern Arizona are of the race *arsipus*. He further concludes that *V. m. arizonensis* described by Goldman (1931) from two miles south of Tule Tanks in Yuma County is a synonym of *V. m. arsipus*.

In the early evening hours this big-eared little fox is rather frequently seen, adjacent to suitable habitat, foraging along the edge of paved or oiled highways apparently feasting on the refuse and dead animals that accumulate in such places.

A male kit fox caught by Blanchard in a wash west of the Castle Dome Mountains on October 24, 1949 weighed 3 pounds 8 ounces.

Urocyon cinereoargenteus scotti Mearns.—During the period June 24 to June 27, 1946 the senior author was at Tinajas Altas, a series of natural "tanks" or rain catchment basins in the Tinajas Altas Range of southwestern Yuma County. Contrary to old legends, the tanks had gone dry and no water was available for game. At 6:26 p.m. on the 24th we noted a gray fox leaving one of the higher tanks (dry) and climbing up into the range over the smooth granite rocks. A moment later another fox followed the first one. At 6:35 p.m. two foxes, presumably the same ones were seen again slowly climbing higher into the range. We assumed that these foxes came in for water and/or food and we know they left without water.

We have found foxes to be common all over the county in suitable localities, but particularly so in and around the rough desert ranges of the region.

Standard measurements in inches of a male secured at Tinajas Altas February 23, 1946 were: 36-14¼-5-2⅞. This animal was sent to the Biological Survey Collection. A male gray fox having an entire weight of 4¾ lbs. and standard measurements in inches of 36¾-15⅝-4¾-3 taken 2/18/47 in the Castle Dome Mountains was sent to the Texas Cooperative Wildlife Collection as was a female caught the same date and place that weighed 5¾ lbs. (entire) and measured as follows: 37-15½-4¾-2⅞.

On April 18, 1947 at the north end of the White Tank Mountains in Engesser Pass, Blanchard trapped a fox containing two unborn pups.

Canis latrans mearnsi Merriam.—We have noted that there is a definite drift of coyotes into the Kofa mountains from the northeastern part of the county. We believe these animals drift into the area along this route from as far as Congress Junction and Aguila.

Blanchard noted a summer concentration of at least 41 deer at Hoodoo Well in the foothills of the eastern Kofa. When ten traps were placed in the vicinity one evening, five coyotes were found caught the next morning.

Coyotes are seen in the highest and roughest parts of the ranges we have patrolled and frequently found along the bottomlands of the river basins. We have also noted that during the daytime in the hot summer months coyotes will lie in the shade very close to the permanent waterholes. During the warmer months these animals have been seen walking in and drinking at waterholes during the daylight hours.

During the dry winter of 1945-1946 when we had a very small percentage of the

normal rainfall, Fish and Wildlife Service hunter James Boswell found that coyotes in the Castle Dome Mountains were eating trapline coyote carcasses.

The coyote's habit of carrying objects while traveling was recorded by the senior author when a coyote was seen carrying an object in its mouth at 3:16 p.m. on November 24, 1944 in the Squaw Peak area of the Kofa Game Range.

Under date of April 29, 1948 Charles C. Sperry reported on three coyote scats collected by refuge personnel on the Kofa Game Range. One of these scats contained deer, another 25% rabbit and 74% deer, and a third contained bighorn.

On January 26, 1946 a temporary refuge employee, James T. Havins, trapped a "blue" coyote on the Cabeza Prieta Game Range just east of the Yuma County line in Pima County. The skin of this off-color coyote was sent to the Biological Surveys Collection.

In April 1947 three gravid coyotes were each found to have three unborn young in them. The young found on April 6 were 7/8" long, those of April 11, were 2½" long, and those found April 24 were 1" long. A male coyote trapped December 17, 1949 weighed 17½ lbs.

Felis concolor browni Merriam.—At this time the mountain lion can be considered a rare mammal in the area. The last lion taken was an old male weighing 125 lbs. trapped February 17, 1944 in the Kofa Mountains by William Casto of the Fish and Wildlife Service. This cat was reported upon by Halloran (1946).

Since 1944 we have had several reports of lions being seen in and about the Colorado River on the Imperial Refuge and along the course of the Gila River east of Yuma. No lions or their tracks have been reported by Fish and Wildlife Service personnel on the game ranges since Casto took the 125 lb. cat near Squaw Peak on the Kofa Game Range.

Merriam (1903) in his original description of this race stated, "The small size of the bullae seems to indicate that the Colorado desert cougar finds his prey more by sight than hearing; and the slender canines and small lateral teeth indicate that he preys on smaller animals than the deer-killing cougar of the uplands." The type of this variety weighed 170 lbs. (Merriam, 1903) and it is entirely possible that certain individuals at least are capable of killing big game. This is indicated by the fact that six lion scats collected in January 1944 in the Kofa Mountains by J. A. Kempton in cooperation with Mr. Casto and reported upon by Charles C. Sperry of the Denver Wildlife Research Laboratory contained remains of rabbit, deer, and mountain sheep.

An interesting newspaper account from the Yuma *Sun*, dated November 24, 1916, tells of a mountain lion trapped by John Jones about three miles west of Yuma. Mr. Jones since stated to Halloran that he gave this male lion, which he estimated to be about four months old, to a circus. The article continues, "This is the first mountain lion captured or killed in this section for many years, that anyone knows anything about." It appears evident that the change in habitat of this section of the Colorado River from untamed and annually flooded bottomlands to cultivated fields has adversely affected the area as far as food and cover for lions are concerned.

Lynx rufus baileyi Merriam.—Bobcats are common in the county and have been for many years if we can judge by the facts that W. W. Holder took one in 1864 at Ehrenberg (Grinnell, 1914, p. 253) and that the intermittent record of bounties paid for many years since 1870 by the Supervisors of Yuma County frequently mention payment for bobcats. We have found bobcats and their sign from the saddles in the tops of the desert mountain ranges to the tropical-like jungles of arrowweeds along the Colorado River. A series of six samples of bobcat droppings collected April 18, 1945 by Halloran 10 miles east of Papago Well just east of the southeastern corner of Yuma County and reported upon by Charles C. Sperry contained parts of snake (*Pituophis*), *Citellus tereticaudus*, *Dipodomys*, rabbit, mouse, and plated lizard (*Gerrhonotus*).

These desert cats exhibit a certain amount of local color variation, some specimens having a grayish cast, other individuals a rufous coloring.

A female carrying two young with crown-rump measurements of 2⅛" trapped by H. J. Johnson had standard measurements in inches of 27-5⅛-6-3. A male trapped the day before in the same area by the same trapper had standard measurements in inches of 33-5½-7⅛-3. A 23½ lb. male caught by Blanchard in the Kofa Game Range during the spring of 1949 is the heaviest bobcat known to us from the study area.

REFERENCES

BENSON, SETH B. 1938—Notes on kit foxes (*Vulpes macrotis*) from Mexico. Proc. Biol. Soc. Washington 51:17-23.

BURT, WILLIAM HENRY 1938—Faunal relationships and geographic distribution of mammals in Sonora, Mexico. Univ. Mich. Mus. Zool. Misc. Publ. 39.

DICE, LEE R. 1943—The biotic provinces of North America. Univ. Michigan Press. viii+78 pp.

GOLDMAN, EDWARD A. 1931—Two new desert foxes. Jour. Wash. Acad. Sci. 21(11):249-251.

———1950—Raccoons of North and Middle America. North American Fauna No. 60.

GRINNELL, JOSEPH 1914—An account of the mammals and birds of the Lower Colorado Valley. Univ. Calif. Publ. Zool. 12(44):51-294.

GRINNELL, DIXON, LINSDALE 1937—Fur-bearing mammals of California. 2 vols. Univ. of California Press.

HALLORAN, ARTHUR F. 1946—A recent record of the Yuma Mountain lion in Arizona. Jour. Mamm. 27(1):89-90.

———1947—Mammals found in a cistern in the Cabeza Prieta Mountains, Arizona. Ibid. 28(1):65.

HOWELL, ARTHUR H. 1906—Revision of the skunks of the genus Spilogale. North American Fauna No. 26.

HUEY, LAWRENCE M. 1937—Descriptions of new mammals from Arizona and Sonora, Mexico. Trans. San Diego Soc. Nat. Hist. 8(25):349-360.

———1942—A vertebrate faunal survey of the Organ Pipe Cactus National Monument, Arizona. Ibid. 9(32):353-376.

MERRIAM, C. HART 1903—Eight new mammals from the United States. Proc. Biol. Soc. Washington 16:73-78.

NICHOLS, A. A. 1943—The natural vegetation of Arizona. Univ. of Arizona Coll. Ag. Tech. Bull. 68 (reprint).

SCHANTZ, VIOLA S. 1949—Three new races of badgers (*Taxidea*) from Southwestern United States. Jour. Mamm. 30(3):301-305.

SHREVE, FORREST 1942—Vegetation of Arizona. Reprinted from Flowering Plants and Ferns of Arizona. U. S. Dept. Ag. Misc. Publ. 423.

SMITH, H. V. 1945—The climate of Arizona. Univ. of Arizona Ag. Exp. Sta. Bull. 197.

WILSON, ELRED D. 1933—Geology and mineral deposits of Southern Yuma County, Arizona. Ariz. Bur. Mines, Geol. Series 7, Bull. 134.

YOUNG AND GOLDMAN 1944—The wolves of North America. American Wildlife Institute, Washington, D. C.

A Comparative Study of the Wing Myology of Certain Passerines

Jeff Swinebroad
Ohio State University, Columbus

Investigations of avian anatomy, especially those in which relationships between anatomy and physiological activity are demonstrated, have been few in number. The phenomenon of flight, one of the most conspicuous and fundamental activities of most birds, justifies further research. An understanding of the structure of the wing must precede any discussion of the physiological activity, and is basic to a knowledge of the behavior pattern of flight.

The purpose of this paper is: 1) To describe the wing myology of four common passerines: *Passer domesticus, Richmondena cardinalis, Zonotrichia albicollis,* and *Melospiza melodia;* and 2) To note apparent phylogenetic variations and functional differences of these species as compared with those whose myology has been described.

The literature in this particular field is largely confined to brief descriptions in general references such as Beddard (1898) *The Structure and Classification of Birds,* and Stresemann (1927-34) in *Aves.* These publications do not cover any one species of bird in appreciable detail. The only major specific investigations of wing myology other than references established primarily for veterinarians (see Chamberlain, 1943), are those by H. I. Fisher (1946), R. W. Shufeldt (1890) and W. H. Burt (1930). Dr. Fisher treated the anatomy, adaptations, and functions of the locomotor apparatus of the Cathartidae. Dr. Shufeldt described in some detail the myology of *Corvus corax sinuatus,* and Dr. Burt discussed the adaptations of the North American Picidae. A. B. Howell explained the homologies of the shoulder musculature of *Gallus gallus* and this work is a standard reference for the nomenclature of that region of the wing (Howell, 1937) More recently a paper has been published on the anatomy of *Coua caerulea* (Berger, 1953). This paper appeared after completion of my investigations, however, the findings reported by Berger in general appear to support conclusions I have reached

Despite Howell's statement that: "The topographical myology of birds is well known, but the homology of their muscles has not been determined in all particulars; the only available reference giving specific and complete information regarding the topography of a passerine is Shufeldt's *Myology of the Raven.*

The facilities of the Ornithology Laboratory of Ohio State University were placed at my disposal for this study, and for this and other invaluable assistance, I wish to express my indebtedness to Dr. L. S. Putnam and Miss Mildred Miskimmen of this institution.

Methods

The species which constitute the source for the investigations in this problem were selected to include the following:

1. Passerines representing different families.
2. A non-migratory and migratory member of one family.
3. Passerines having flight patterns different from species whose wing myology has been described.
4. Species, the wing myology of which has apparently not been previously described.

Homology of the muscles was determined by:
1. Relative position of nerves, muscles, and bones.
2. Origin and attachment of muscles.
3. Functions of muscles.

The specimens were preserved in a mixture of alcohol and glycerine. Observations and illustrations were made at the time of dissection. Functions of muscles were determined by observations on the origins, attachments and contractibility of the muscles, with consideration given to the limitations of bone structure, ligaments, and counter-acting or restricting muscles. In many cases it was possible to manipulate the muscles and produce the same action as in a normal contraction.

No detailed descriptions of innervations for muscles other than those of the shoulder region were made since the homologies of the musculature of forearm and hand were evident.

The nomenclature of the shoulder region used in this paper is adapted from Howell (1937). The nomenclature of the muscles of the forearm and hand is adapted from Shufeldt (1890) and Fisher (1946). The nomenclature of the parts of the bones is that of Howard (1929).

MATERIAL EXAMINED

Passer domesticus (English Sparrow): Preserved wings—adult male, 3; adult female, 2.

Richmondena cardinalis (Cardinal): Preserved wings—adult male, 4; adult female, 1. Fresh material—adult male, 2.

Zonotrichia albicollis (White-throated Sparrow): Preserved wings—adult male, 4; adult female, 4; immature (sex undetermined), 1. Fresh material—adult female, 2.

Melospiza melodia (Song Sparrow): Preserved material—adult male, 1.

Miscellaneous: One specimen each of *Corvus brachyrhynchos*, *Dendroica nigrescens*, and *Toxostoma rufum* were examined but not included in this paper.

MUSCLES OF THE SHOULDER

TABLE 1.—Origins of M. serratus posterior, deep layer

	Second Free Rib	First True Rib	Second True Rib	Third True Rib	Fourth True Rib
Vultures[1]			×	×	×
Woodpeckers[2]		×			
Raven[3]	×	×	×		
English Sparrow	×	×			
Cardinal	×	×			
Song Sparrow	×	×			
White-throated Sparrow	×	×			

1 Fisher (1946), 2 Burt (1930), 3 Shufeldt (1890).

Dorsal Division

PART I. SUPRAZONAL—for innervations of these muscles see figs. 1-3.

M. SERRATUS METAPATAGIALIS
(dermo-ulnaris of Shufeldt)

Origin.—Fleshy, from the fascia covering the ribs at the anterior ventral margin of the origin of M. serratus posterior, superficial layer.

Insertion.—Tendinous, on the anterior proximal end of the posterior patagial membrane, and fleshy on the integument.

Function.—Aids in maintaining position of posterior brachium and may act as a weak extensor of the forearm.

Description.—A thin, band-like muscle of the same consistency as M. serratus posterior, deep layer. Toward the distal portion of serratus metapatagialis the fibers of the muscle form a more rounded belly.

Discussion.—This muscle does not differ significantly in any of the species examined, nor does it appear in these birds to be at variance with previous descriptions in other species.

M. SERRATUS POSTERIOR, superficial layer
(serratus magnus anticus of Shufeldt)

Origin.—Fleshy, from the ventral portion of the vertebral rib of ribs 2, 3, 4, and 5 (in all but the Song Sparrow). In the Song Sparrow the origin is similar but from ribs 2, 3, and 4 only.

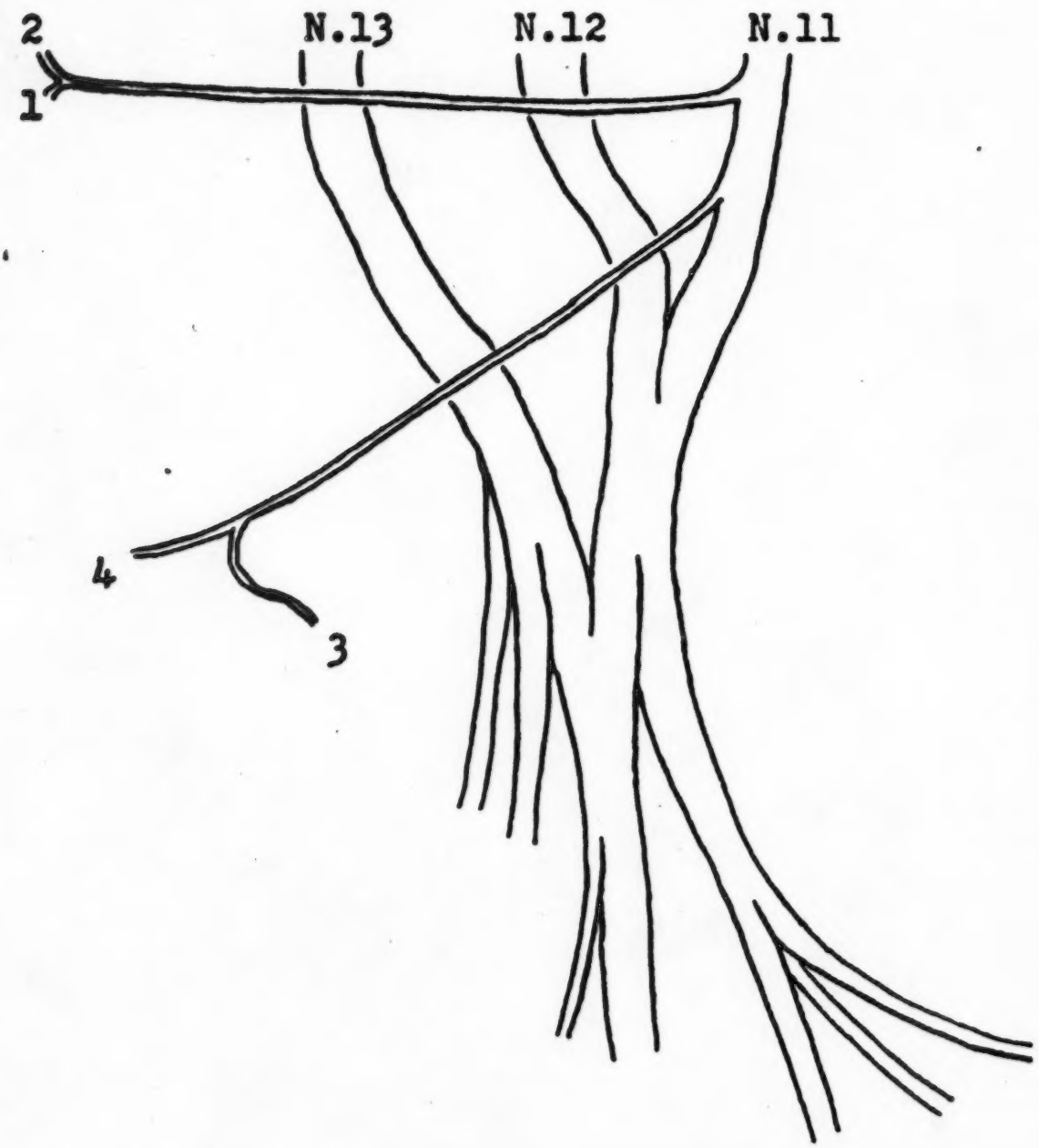


Fig. 1.—Brachial plexus of right wing of *Passer domesticus* (dorsal view). Innervation: 1. serratus profundus; 2. serratus anterior; 3. serratus posterior, deep layer; 4. serratus posterior, superficial layer.

Insertion.—Fleshy, on the ventral margin of the blade of the scapula. In the case of the White-throated Sparrow the insertion is more toward the external side while in the Cardinal the muscle inserts on the inner ventral margin of the scapula blade.

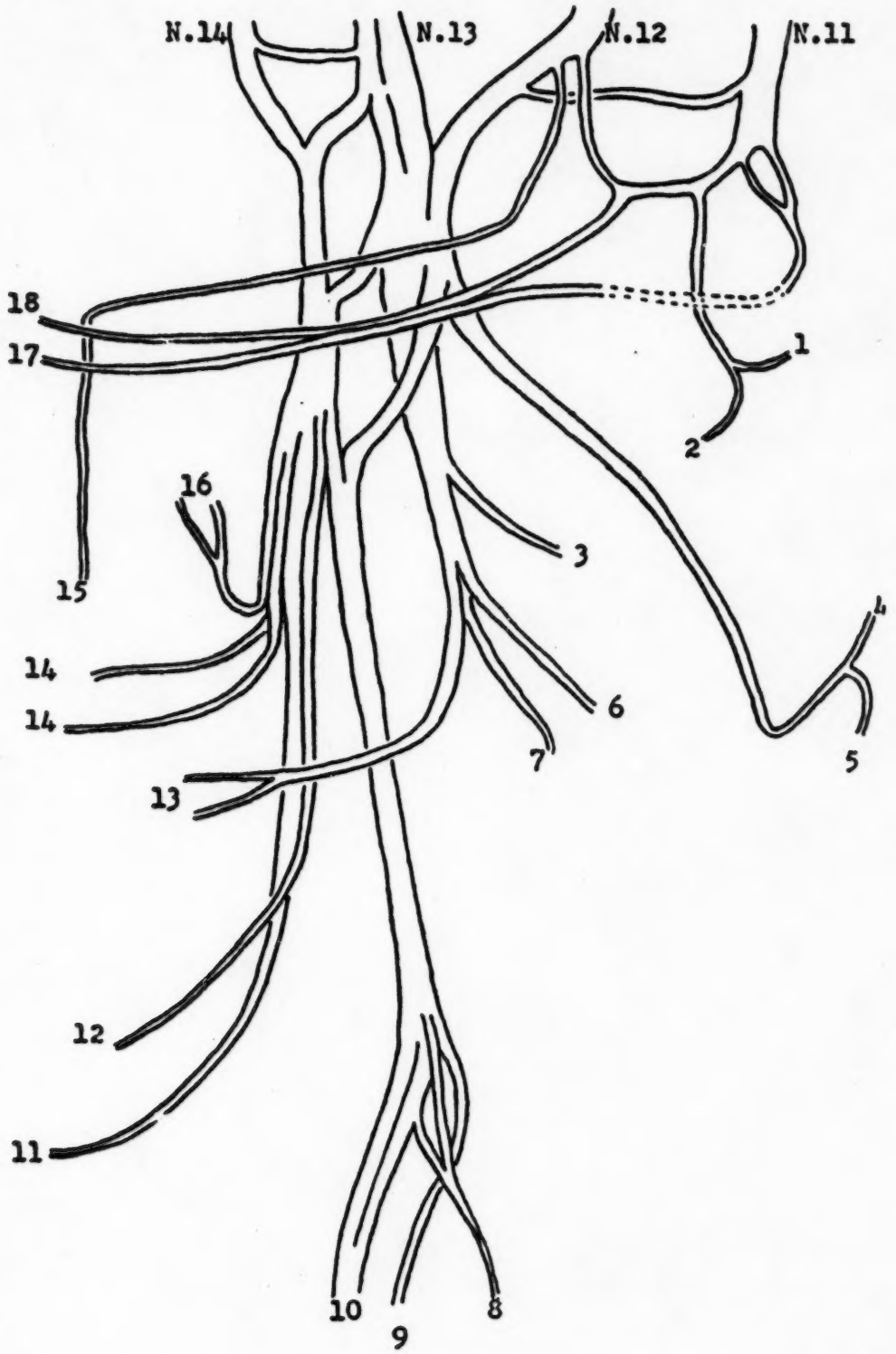


Fig. 2.—Brachial plexus of right wing of *Richmondena cardinalis* (dorsal view). Innervation: 1. rhomboideus superficialis; 2. rhomboideus superficialis; 3. subscapularis; 4. supracoracoideus; 5. subcoracoideus; 6, 7. dorsalis scapulae; 8. deltoid, distal region; 9. latissimus dorsi; 10. deltoid, anterior region and tensor patagii; 11. biceps, triceps and muscles of forearm and hand; 12. muscles of forearm and hand; 13. dorsalis scapulae; 14. pectoralis superficialis; 15. serratus posterior, deep layer; 16. coracobrachialis posterior; 17. serratus profundus; 18. rhomboideus profundus. Dotted line indicates probable nerve connection.

Function.—Moves the scapula inward and ventrally, or conversely expands the chest cavity by pulling the ribs upward and outward.

Description.—This was the largest muscle of the serratus complex in all species examined. It was proportionately smaller in the Song Sparrow than any of the other species. A few fibers were found to blend with the posterior margin of M. rhomboideus profundus near the insertion of the latter. In the Cardinal a few fibers blended with M. dorsalis scapula.

Discussion.—The area of insertion of this muscle was found to be variable. In the White-throated Sparrow, the length of the line of insertion varied from a millimeter or less up to four or five millimeters. Correspondingly, this was found to be true with the other species examined. This muscle appears to have a wider area of origin in three of these passerines than in the woodpeckers (Burt, op. cit.), or vultures (Fisher, op. cit.). In the Song Sparrow, however, the origin agrees with descriptions of those non-passerines and with the origin as described for the Raven (Shufeldt, op. cit.). The superficial layer arises by three or four digitalions as the case may be, which merge almost immediately into the broad fanshaped body of this muscle.

M. SERRATUS POSTERIOR, deep layer
(thoraco-scapularis of Shufeldt)

Origin.—Fleshy, by two heads, the ventral head originating from the ventral lateral portion of the second free rib, and the dorsal head arising from the lateral surface of the ventral portion of the vertebral rib (ventral to the uncinate process) of the first true rib.

Insertion.—Fleshy, on the internal surface of the blade of the scapula between the arms of N. subscapularis.

Function.—Moves the scapula ventrally and posteriorly, or draws the attached ribs forward and outward. Any action caused by this muscle is probably weak. The two heads of this muscle unite to form one band-like muscle before it disappears between the arms of M. subscapularis. The origin of this muscle appears to be highly variable in different species of birds. Some idea of this variability is presented in table 1.

Description.—See figure 6.

Discussion.—The action of this muscle is of minor importance as far as contributions to flight are concerned, and at present, the exact effect this muscle has on inspiration is unknown.

M. SERRATUS ANTERIOR
(serratus parvus anticus of Shufeldt)

Origin.—Fleshy by two heads; one from the dorsal lateral surface of the vertebral rib of the first true rib, and the other from a similar position on the second free rib. A few fibers arise from the intervening fascia. In the English Sparrow the origin is by one head from the second free rib. In the Song Sparrow the origin is by one head from the first true rib.

Insertion.—Fleshy, on the internal surface of the blade of the scapula immediately distal and ventral to the insertion of M. serratus profundus. Some fibers of M. serratus anterior merge with serratus profundus near this insertion and the two muscles seem to insert together.

Function.—Moves the scapula anteriorly, medially and slightly ventrally or draws attached ribs outward.

Description.—See figure 6.

Discussion.—Serratus anterior is another highly variable muscle. According to Shufeldt (op. cit., p. 104), the origin of this muscle in the Raven is more extensive, and the insertion appears to be more distally located. The function of serratus anterior is similar in the passerines that have been examined. In the vulture, however, the position of the muscle is such that its contraction moves the scapula posteriorly, which is the reverse of the situation that occurs here. Since in all types of flight the scapula remains relatively immovable it is difficult to analyze these variations of M. serratus anterior according to function. Its position and that of M. serratus profundus suggests that the forward movement of the scapule, the ultimate result of which is an increase in the lift of the wing, is of some significance in flapping flight (see M. pronator brevis).

M. SERRATUS PROFUNDUS
(levator scapulae of Shufeldt)

Origin.—Variable in all species examined; usually fleshy from the dorsal-lateral surface of the second free rib and usually from the transverse process of the last cervical

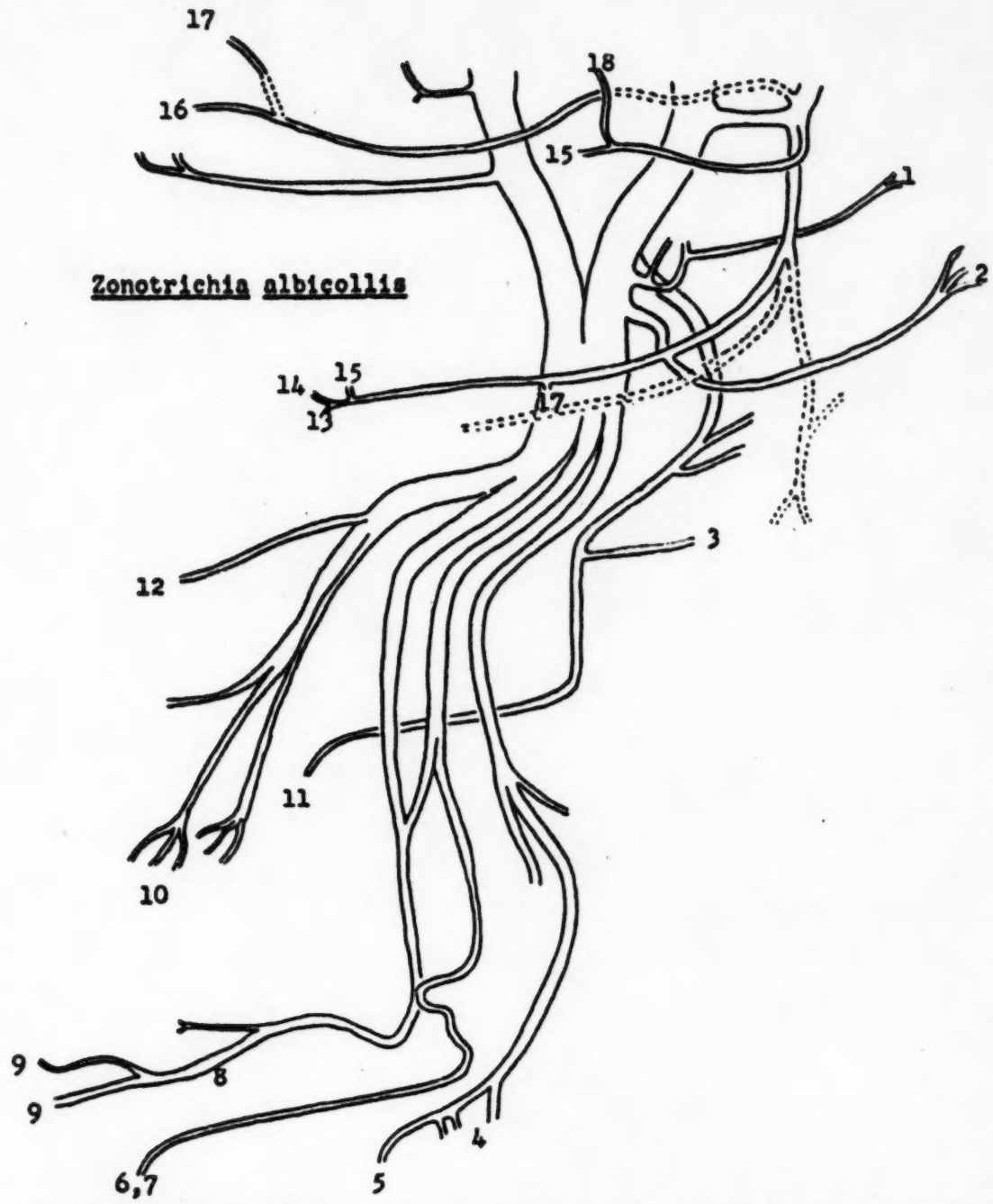


Fig. 3.—Brachial plexus of right wing of *Zonotrichia albicollis* (dorsal view). Innervation: 1. subscapularis; 2. dorsalis scapulae; 3. subcoracoideus; 4. deltoid major and deltoid minor; 5. tensor patagialis brevis and longus; 6. muscles of forearm and hand; 7. biceps; 8. triceps; 9. muscles of forearm and hand; 10. pectoralis superficialis; 11. supracoracoideus; 12. coracobrachialis posterior; 13. rhomboideus superficialis; 14. rhomboideus profundus; 15. serratus profundus; 16. serratus posterior, superficial layer; 17. latissimus dorsi; 18. serratus anterior. Dotted lines indicate probable nerve connection.

vertebra. Occasionally the origin may include the last two cervical vertebrae, and rarely may exclude the origin from the second free rib. This latter condition was found only in the White-throated Sparrow.

Insertion.—Fleshy, on the internal surface of the blade of the scapula (see illustration).

Function.—Moves scapula anteriorly and medially.

Description.—This is the second largest muscle of the serratus complex and appears to be essentially similar in all the species that have been examined.

Discussion.—M. serratus profundus acting alone would elevate the distal end of the

scapula and thus bring about a depression of the leading edge of the wing (see M. serratus anterior).

M. RHOMBOIDEUS SUPERFICIALIS
(trapezius of Shufeldt)

Origin.—Fleshy; in the English Sparrow from the neural spines of thoracic vertebrae 1, 2, and 3, and from the neural spines of the last two cervical vertebrae; in the Cardinal from the neural spines of thoracic vertebrae 1, 2, 3, 4, and 5, and the last two cervical vertebrae; in the other species from the neural spines of the first five thoracic vertebrae.

Insertion.—Fleshy, on the entire dorsal margin of the blade of the scapula.

Function.—Moves scapula medially and elevates shoulder. According to Fisher,

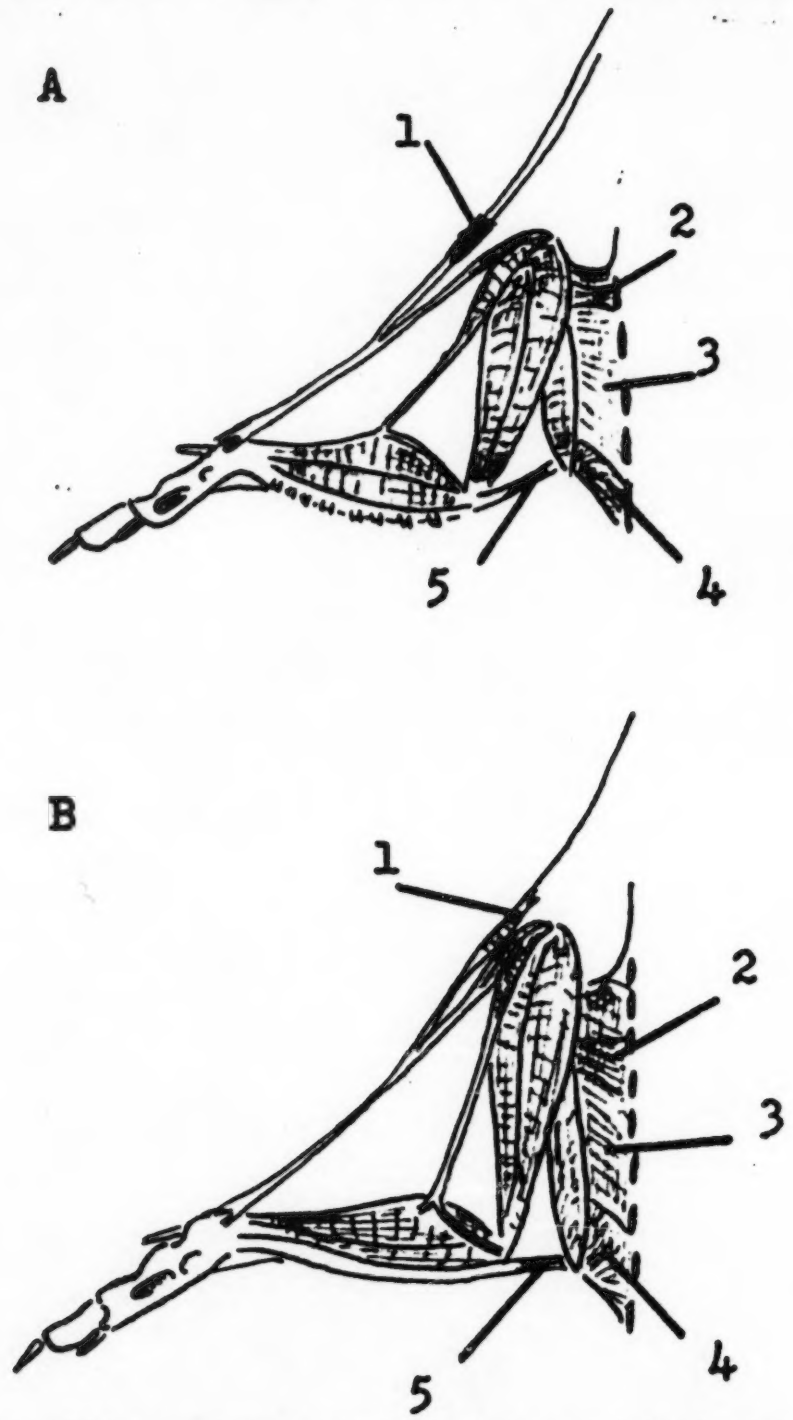


Fig. 4.—Superficial muscles of the shoulder and patagium.—*A. Zonotrichia albicollis.* 1. dermo-tensor patagii; 2. latissimus dorsi; 3. rhomboideus superficialis; 4. rhomboideus profundus; 5. serratus metapatagialis. B. *Richmondena cardinalis.* 1. dermo-tensor patagii; 2. latissimus dorsi; 3. rhomboideus superficialis; 4. rhomboideus profundus; 5. serratus metapatagialis.

"Tension in this muscle is important in maintaining the position of the bones when muscles arising from the bones contract to move the humerus." (Fisher, op. cit., p. 582.)

Description.—The anterior part of this muscle is about half again as thick as the sheet-like posterior portion. Fibers of this muscle are arranged in an antero-lateral direction (see M. rhomboideus profundus).

Discussion.—No appreciable difference was noted.

M. RHOMBOIDEUS PROFUNDUS
(rhomboideus of Shufeldt)

Origin.—Fleshy; in the English Sparrow from the neural spines of thoracic vertebrae 1, 2, 3, 4, and 5, and the last cervical vertebrae; in the Cardinal from the neural spines of all the thoracic vertebrae, and from the first two lumbar vertebrae; in the remaining species from the neural spines of thoracic vertebrae 2, 3, 4, and 5.

Insertion.—Fleshy, on the internal side of the dorsal margin of the blade of the scapula, usually occupying only the distal one-third of that area, and lying ventral to the insertion of M. rhomboideus superficialis.

Function.—Moves the scapula medially, anteriorly, and elevates the scapula. As noted by Fisher (op. cit., p. 583), "Both M. rhomboideus profundus and M. rhomboideus superficialis aid in raising the shoulder. This is important in raising the entire wing while the longitudinal axis of the wing remains horizontal. In soaring and gliding the wing may be raised at its base; this lowers the position of the center of gravity relative to the supporting plane and provides for greater stability."

Description.—The fibers of this muscle extend in a postero-lateral direction. Both M. serratus posterior, superficial layer, and M. serratus profundus send fibers to rhomboideus profundus.

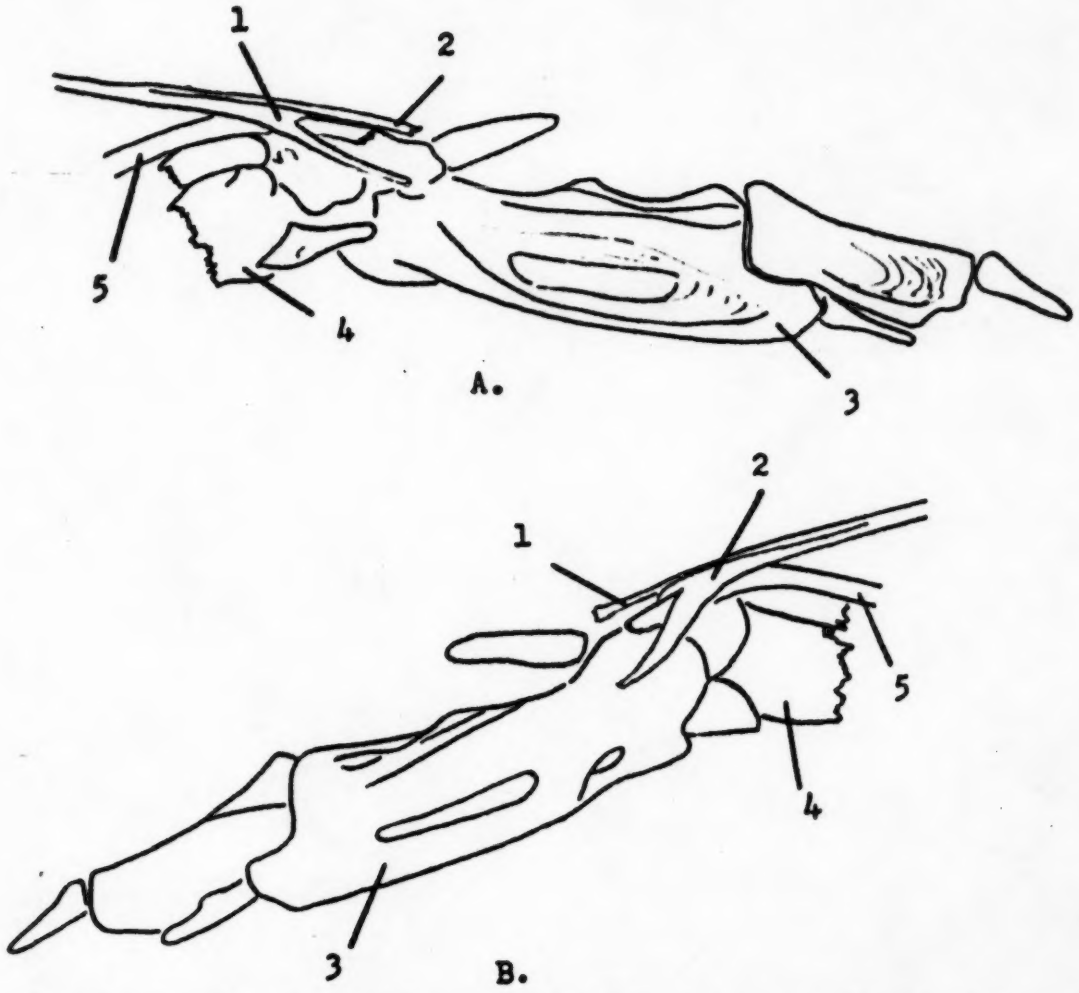


Fig. 5.—Insertion of patagial muscles of *Richmondena cardinalis*.—A. Palmar view; B. Anconal view. 1. M. tensor-patagialis longus; 2. tendon traceable to M. dermo-tensor patagii; 3. carpometacarpus; 4. ulna; 5. tendon of M. extensor metacarpi radialis.

Discussion.—No appreciable differences were noted in any of the species examined.

PART II. SHOULDER—for innervations of these muscles see figures 1-3.

M. LATISSIMUS DORSI

Origin.—Fleshy; in the English Sparrow from the posterior part of the neural spine

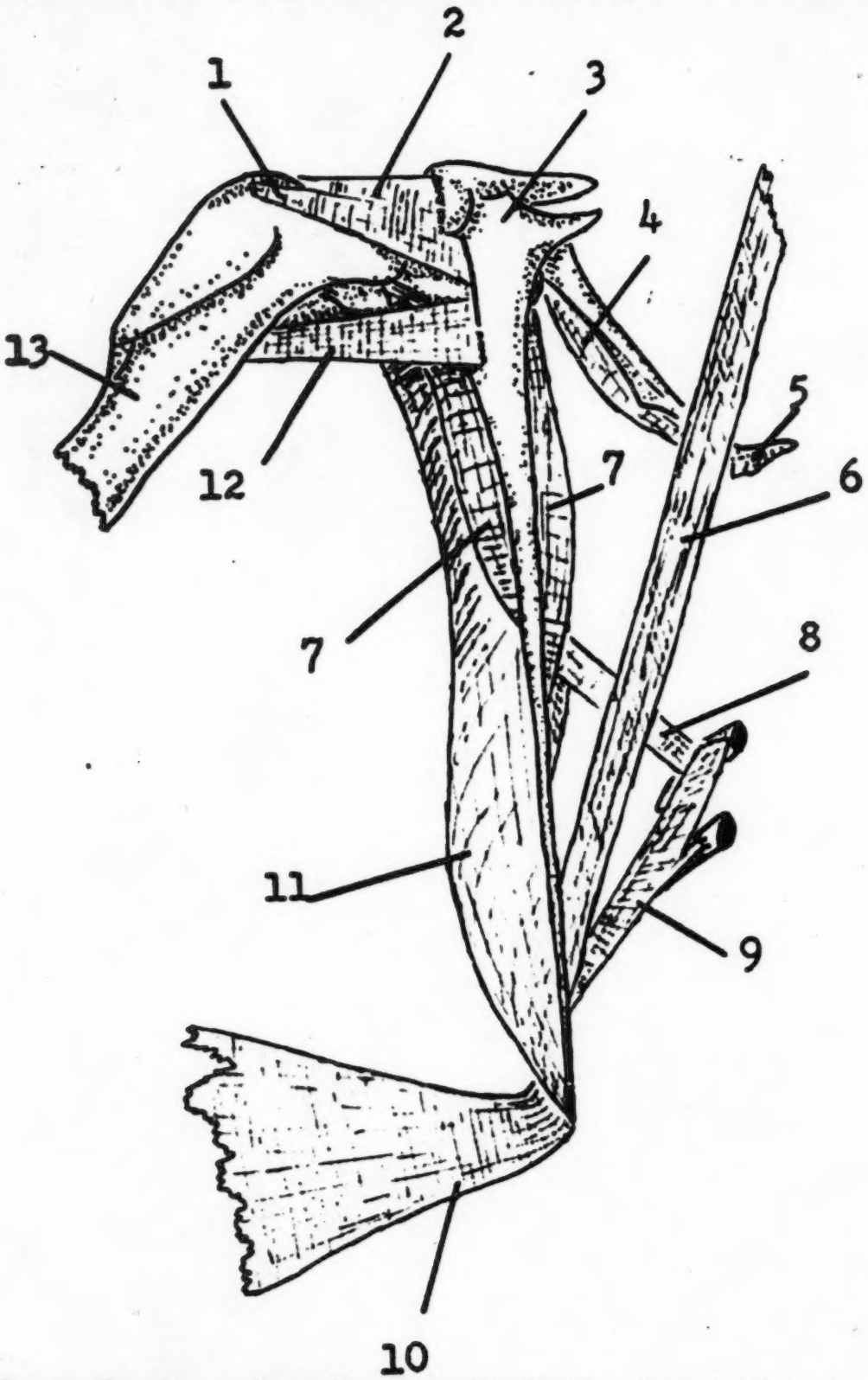


Fig. 6.—Scapular muscles of *Zonitrichia albicollis* (deep layer, dorsal view). 1. M. deltoid minor; 2. M. coracobrachialis anterior; 3. scapula; 4. subcoracoideus; 5. coracoid; 6. M. serratus profundus; 7. M. subscapularis; 8. M. serratus posterior, deep layer; 9. M. serratus anterior; 10. M. serratus posterior, superficial layer; 11. M. dorsalis scapulae; 12. M. proscapulohumeralis; 13. humerus.

of the last cervical vertebra, from the neural spine of the first thoracic vertebra, and from the posterior portion of the neural spine of the second thoracic in the Cardinal from the neural spines of thoracic vertebrae 1, 2, and 3; in the White-throated Sparrow from the neural spine of the first thoracic vertebra; in the Song Sparrow from the neural spines of the first thoracic and last cervical vertebrae.

Insertion.—Fleshy, on the dorsal surface of the humerus passing between the heads of M. triceps and M. deltoid major to the insertion (see illustrations).

Function.—Pulls humerus inward, aiding the flexing of the upper arm, and rotating the anterior edge of the humerus upward.

Description.—See figure 9.

Discussion.—In these species and in the woodpeckers this muscle is composed of only a single part. In the vultures (Fisher, op. cit.) and in *Gallus gallus* (Howell, op. cit.) this muscle is double. In the Cardinal M. latissimus dorsi is heavier than in the other fringillids examined.

M. DORSALIS SCAPULAE
(teres et infraspinatus of Shufeldt)

Origin.—Fleshy, from the entire lateral surface of the blade of the scapula distal to the origin of M. subscapularis, from the ventral margin of the distal portion of the blade of this scapula, and from a restricted area of the inner ventral margin of the distal portion of the blade of the scapula.

Insertion.—Tendinous, on the ulnar tuberosity of the humerus palmar to the insertion of M. subscapularis.

Description.—See figure 6.

Discussion.—In all of the species examined this was the largest and most powerful muscle of the scapula.

M. DELTOID MAJOR

Origin.—Long head: Fleshy from the head of the furcula posterior to the origin of M. tensor patagii and extending from the dorsal most margin of the furcula over and ventrally from the internal margin of the head of that bone. Short head: Fleshy from the deltoid surface of the humerus, from the os humero-scapulae, and tendinous by a long tendon from the acromion of the scapula. In the White-throated Sparrow this origin from the scapula appeared to be part of the origin of the long head of M. deltoid major.

Insertion.—Long head: Fleshy, on an area proximal and dorsal to the external condyle of the humerus. Short head: Tendinous, on the proximal margin of the ectepicondylar prominence. This insertion is located dorsally to that of the long head.

Function.—Flexes and elevates the humerus. The two heads are connected by the covering fascia and intermingling fibers; however, they may work more or less independently, as suggested by the separate innervation. The long head, because of its more posterior position and longer power arm, is probably the major contributor in flexion of the humerus, but acts with the short head in elevating the humerus.

Description.—See figures 8 and 9.

Discussion.—This muscle, of varying size in birds, attains its largest bulk in the accipiters and passerines. In the case of the four species included in this paper, M. deltoid major had the greatest bulk of any of the muscles on the humerus. The long power arms of the deltoid in these species, coupled with the short humerus, indicate that there is an increase in the power of elevation of the humerus of these birds. This is correlated with the fast flapping flight and relatively large wing area of the fringillids and ploceids, although consideration of this point must include M. supracoracoideus, proscapulohumeralis, proscapulohumeralis brevis, and triceps. Also correlated with the flapping flight is an increased ability to pull the humerus posteriorly, which is augmented by increased power of action of M. deltoid major. It is interesting to note that in vultures M. deltoid major is shorter and its action is less powerful. This is associated with the soaring type of flight (Fisher, op. cit., p. 616). An intermediate condition exists in the woodpeckers (Burt, op. cit., p. 491). In the White-throated Sparrow a few fibers from M. triceps join the tendon of the short head of M. deltoid major. In none of the other species was any connection noted between M. triceps and deltoid, except that of the enveloping fascia.

M. DELTOID MINOR
(scapulo-humeralis of Shufeldt)

Origin.—Fleshy, from the external surface of the acromion of the scapula, proximal and ventral to the origin of M. proscapulohumeralis.

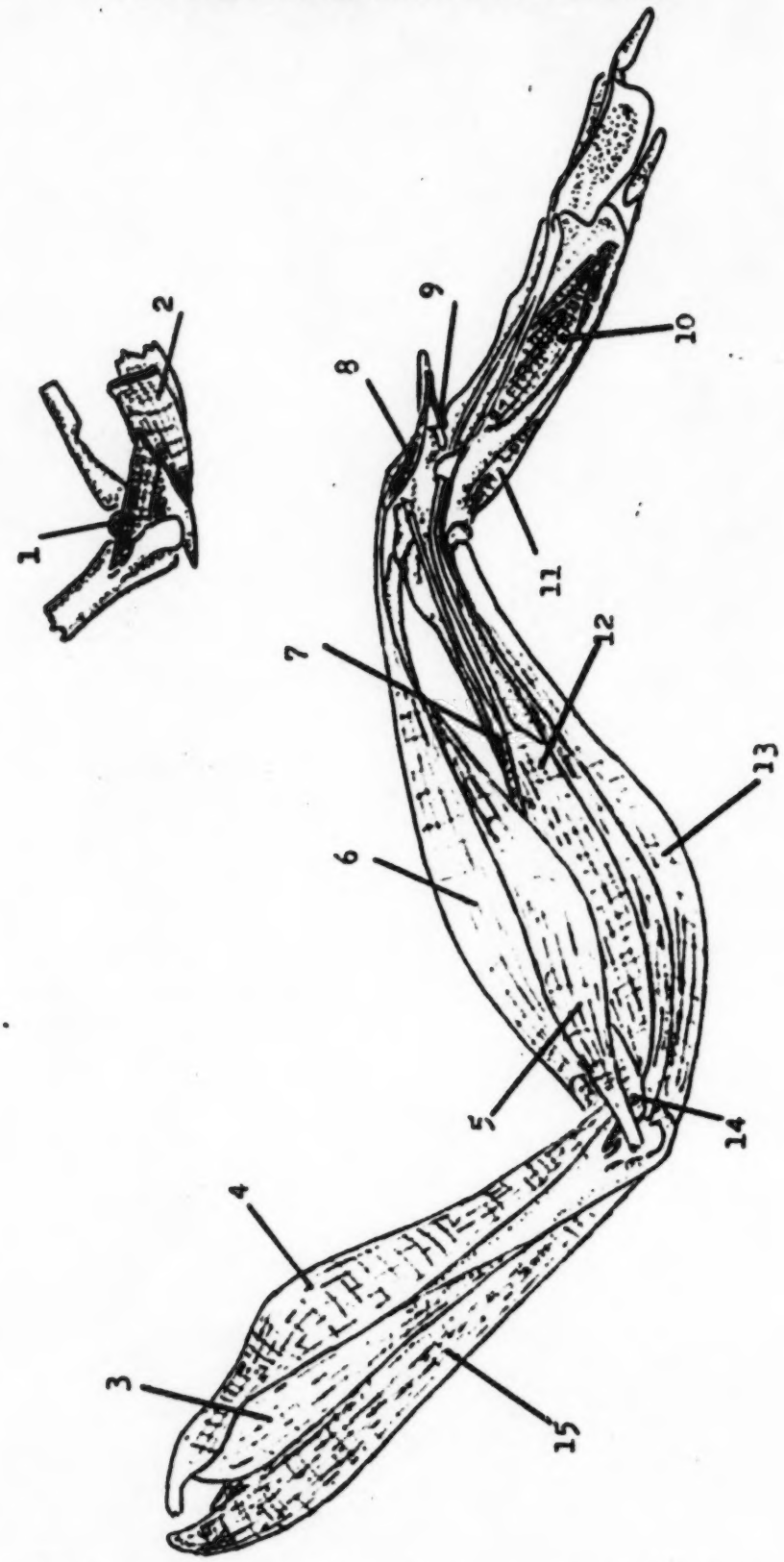


Fig. 7.—Superficial muscles of the forearm and hand of *Zonotrichia albicollis* (palmar view). 1. M. brachialis; 2. M. flexor digitorum profundus; 3. M. triceps; 4. M. biceps; 5. M. pronator brevis; 6. M. extensor metacarpi radialis; 7. M. flexor carpi ulnaris brevis; 8. M. abductor pollicis; 9. M. adductor pollicis; 10. M. interosseus palmaris; 11. M. flexor digiti III; 12. M. flexor digitorum profundus; 13. M. flexor carpi ulnaris; 14. M. pronator longus; 15. M. deltoid.

Insertion.—Fleshy, on the anconal surface of the head of the humerus.

Function.—Elevates anterior margin of humerus, acts with M. coracobrachialis anterior as a weak extensor of the upper arm.

Description.—Together with coracobrachialis anterior this muscle forms a sheaf of fibers covering the proximal portion of the head of the humerus and overlying the insertion of M. supracoracoideus (see figure 9).

Discussion.—M. deltoid minor is of similar structure and function in all of the species examined in this study, and agrees in general with the descriptions of it for the vultures (Fisher, op. cit., p. 583) and the woodpeckers (Burt, op. cit., p. 488). Shufeldt (op. cit., p. 87) describes the insertion of this muscle as follows: ". . . its fibers form a narrow flattened ribbon, that passes over the top of the shoulder joint, parallel to the upper margin of the larger portion of the deltoid, to become inserted on the palmar aspect of the humeral head, directly between the insertions of the pectoralis major and secundus." The function of the deltoid minor would remain unchanged by such an insertion as Shufeldt describes; however, the increased length of power arm would result in a stronger action by this muscle in the Raven. Although deltoid minor is anastomosed for most of its length with M. coracobrachialis anterior, these muscles retain their separate innervations, and are presumed to retain independent action. Fisher (op. cit., p. 583) states that, "This muscle probably comes into play on the recovery stroke of the wing, at which time the above movements [elevation of humerus, raising of anterior end of wing, anterior movement of humerus] occur simultaneously."

M. PROSCAPULOHUMERALIS
(supraspinatus of Shufeldt)

Origin.—Fleshy, from the external surface of the neck of the scapula, distal to the insertion of M. deltoid minor.

Insertion.—Fleshy, on the anconal surface of the humerus distal to the pneumatic foramen.

Function.—Flexes humerus, aids in elevation of humerus, depresses anterior edge of the wing.

Description.—This band-like muscle passes between the internal and external heads of M. triceps to the insertion.

Discussion.—According to Fürbringer (1888), this muscle is frequently absent in some groups of birds. It is inseparable from M. subscapularis in the vultures (Fisher, op. cit., p. 584), and appears to be similar in the woodpeckers (Burt, op. cit., p. 488) and passerines.

M. PROSCAPULOHUMERALIS BREVIS
(teres minor of Shufeldt)

Origin.—Fleshy, from the internal proximal surface of the acromion of the scapula.

Insertion.—Tendinous, on the middle of the ulnar tuberosity in common with the insertion of M. subscapularis (Cardinal) or fleshy, near the ligamental furrow on the palmar head of the humerus proximal to and blended with the insertion of M. subscapularis.

Function.—Draws the palmar surface of humerus inward, and in so doing depresses the anterior edge of the wing. Probably the most important function of this muscle is the retention of the humerus in the glenoid facet.

Description.—This thick fan-shaped muscle is easily mistaken for a part of M. subscapularis. In descending to its insertion on the humerus the body of brevis meets the surface of M. subcoracoideus and in some cases a few fibers are exchanged between these two. The general impression is that M. subscapularis, proscapulohumeralis brevis, and subcoracoideus are all one large U-shaped muscle, the arms of which originate on the scapula and the coracoid and which inserts on the humerus.

Discussion.—This muscle is similar in structure and function in the passerines that have been examined and appears to be similar to that in the woodpeckers (Burt, op. cit., p. 489).

M. SUBSCAPULARIS

Origin.—Fleshy, from the proximal part of the blade and the distal portion of the neck of the scapula, occupying a portion of both the internal and external surfaces of the blade of the scapula, and fleshy, from the ventral surface of the os humeroscapulae. The origin on the internal surface of the blade of the scapula is from two heads, one passing along the dorsal portion of the blade, and the more posteriorly extending head passing along the ventral portion of the blade. M. serratus posterior, deep layer inserts on the scapula between these two heads.

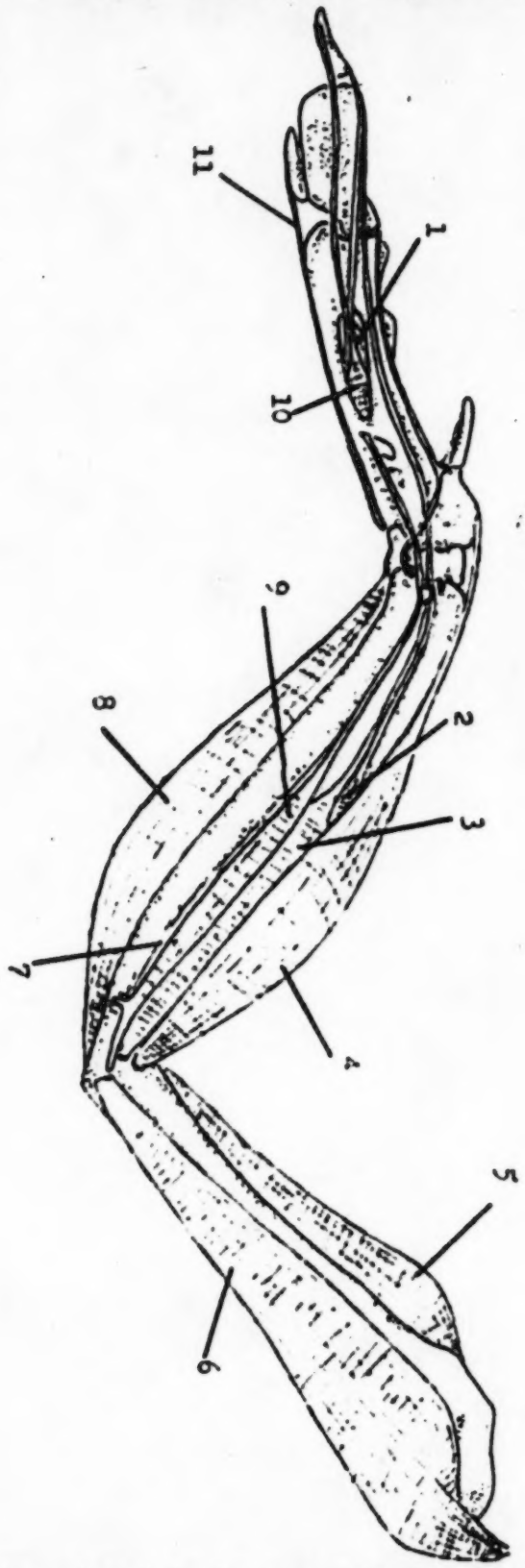


Fig. 8.—Superficial muscles of the forearm and hand of *Zonotrichia albicollis* (anconal view). 1. M. interosseus palmaris; 2. M. extensor indicis longus. 3. M. extensor digitorum communis; 4. M. extensor metacarpi radialis; 5. M. biceps; 6. M. deltoid; 7. M. anconeus; 8. M. flexor carpi ulnaris; 9. M. flexor metacarpi radialis; 10. M. interosseus dorsalis; 11. M. flexor digiti III.

Insertion.—Tendinous by a short thick tendon on the ulnar tuberosity of the humerus (see M. proscapulo humeralis brevis).

Function.—Rotates the humerus, elevating the anterior margin and aids in maintaining humerus in glenoid facet.

Description.—See figure 6.

Discussion.—A large, compact muscle not differing significantly in the species examined (see M. proscapulohumeralis brevis).

PART III. ELBOW DERIVATIVES

TRICEPS

Origin.—Scapular head; fleshy, from the external surface of the head of the scapula extending in an area from the acromion toward the glenoid facet. Internal and external head; fleshy, by two heads from the anconal surface of the humerus, one head passing on each side of the pneumatic fossa of the humerus and internal and external to the insertion of M. proscapulo humeralis.

Insertion.—Mixed fleshy and tendinous, on the posterior surface olecranon of the ulna.

Function.—Extends the forearm (see discussion).

Description.—See figures 7, 8, and 9.

Discussion.—The powerful triceps varies little in flapping flight birds. The variations that are present appear to be correlated with the flying ability of the bird. A strong scapular head of this muscle situated in a posterior position aids in flexing the humerus, when the extensor action of M. triceps is prevented by flexor antagonis muscles. Such development is present in the Cardinal, White-throated Sparrow, Song and English sparrows, and is also noted in other species according to various authors. Strong development of the triceps aids in maintaining the wing in a partly flexed condition as occurs in the short gliding strokes typical of many small passerines. The scapular head is practically an independent muscle as fibers from the internal and external heads join it only at its tendinous end.

Ventral division

PART I. INFRAZONAL

M. STERNOCORACOIDEUS
(subclavius of Shufeldt)

Origin.—Fleshy, from the ventral side of the lateral cranial process of the sternum.

Insertion.—Fleshy, on the dorsal surface of the distal portion of the coracoid (see figure 7).

Function.—Maintains position of the coracoidal facet of sternum.

Description.—A flat muscle which appears to be of similar structure in birds having a flapping type of flight.

Discussion.—No appreciable difference was noted.

PART II. SHOULDER

M. PECTORALIS SUPERFICIALIS
(pectoralis major of Shufeldt)

Origin.—Fleshy, from the ventral posterior face of the sternum from the area not occupied by M. supracoracoideus and M. coracobrachialis posterior, and from the entire length of the ventral portion of the keel of the sternum, and along the entire length of the lateral margin of the furcula.

Insertion.—Fleshy and tendinous on the entire palmar aspect of the deltoid crest.

Description.—Shufeldt (op. cit., p. 70) describes a two part condition existing in the Raven writing that: "The posterior surface of the pectoralis major is far more tendinous in its structure than its anterior. . . ." Examination failed to reveal any very definite division of this muscle in the included species; however, it was noted that at the region of insertion on the deltoid crest of the humerus two layers could be distinguished. The more superficial of the two inserted anteriorly on the deltoid crest, the more posterior inserted by means of a thin tendon on the posterior region of the deltoid crest. Beyond the immediate area of insertion these two layers were indistinguishable. The double innervation noted for this muscle suggests, nevertheless, that there may be two somewhat independently functioning parts.

Discussion.—The insertion of M. pecoralis superficialis suggests that the anterior edge of the wing would be depressed on the downstroke. According to Fisher (op. cit., p. 577), "If the wing were held horizontally and depressed, air would escape past both edges, resulting in turbulence in front of the wings; the only possible force would be vertically upward. By depressing the anterior edge the air mass is cleanly divided, and no air escapes past the anterior edge. Further, a forward motion is imparted to the body as the wing is pulled posteriorly in the later phases of the downstroke." Photographs of

birds in level flight (Queeny, 1947; Hosking and Newberry, 1949; Storer, 1948; Aymar, 1935) reveal that a contrary action appears to be true. On the downstroke of the wing, the inner wing slopes up from the posterior to anterior providing lift, while the outer wing, through action of muscles and feathers, slopes in the opposite direction, providing forward motion (Storer, op. cit.). Also as the wing is lowered the bird is moving forward, thus the wing on its downward beat is meeting the air stream at an angle. The streamlined shape of the wing with its reinforced leading edge and numerous feather wing-slots forces the air to flow over the leading edge and upper surface of the wing. The humerus appears to be held in a partly flexed position during flight. Observations on the action

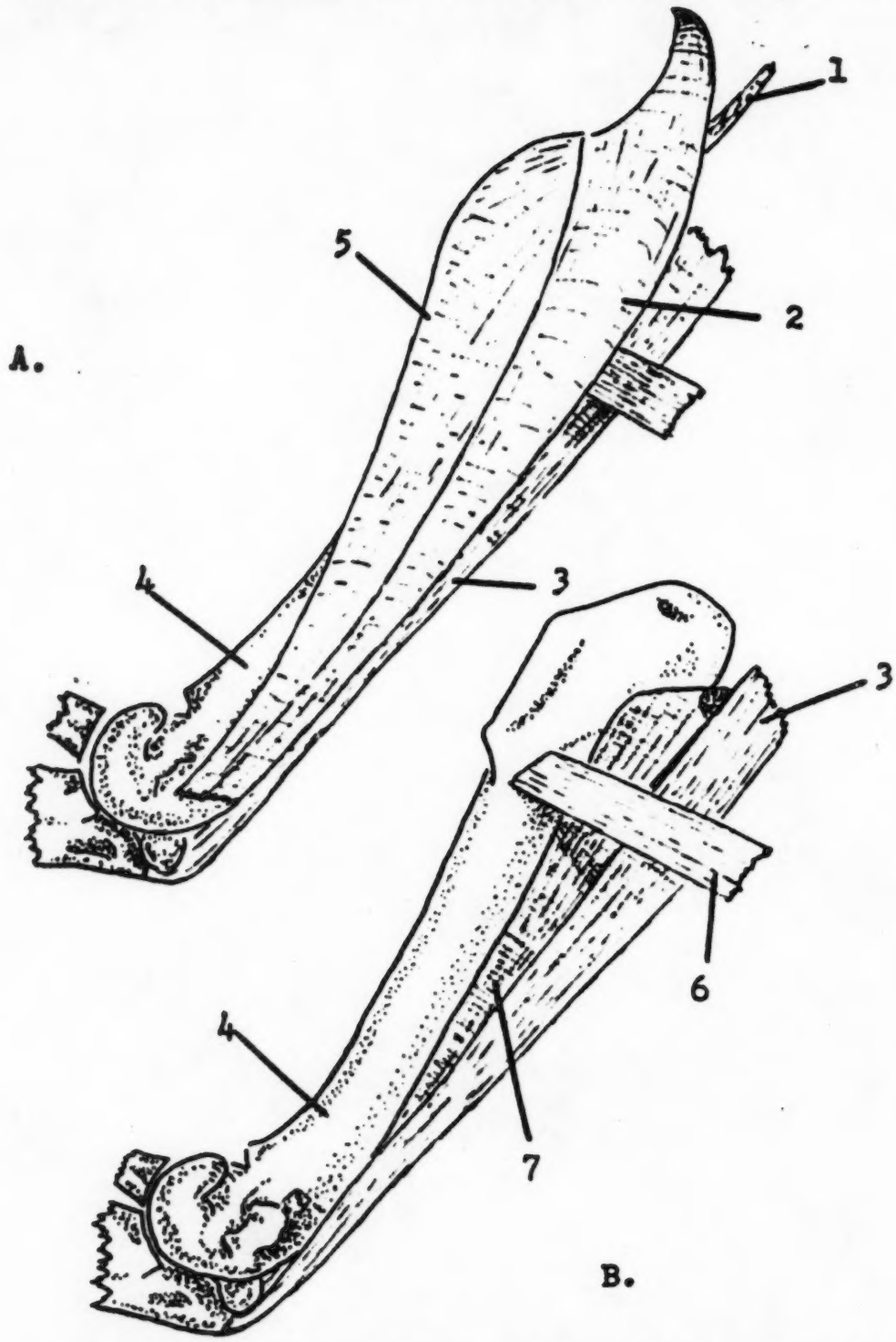


Fig. 9.—Deltoid and triceps of *Richmondena cardinalis*.—A. Dorsal view; B. Dorsal view (deltoid removed). 1. tendon of short head—M deltoid major; 2. long head—M. deltoid major; 3. scapular head—M. triceps; 4. ulna; 5. short head—M. deltoid major; 6. M. latissimus dorsi; 7. internal and external heads—M. triceps.

of M. pectoralis superficialis, when this flexed condition prevails, indicates that the muscle's contraction results in a downward movement of the wing as a whole with little or no inclination of the leading edge. The latter action would fully ensue only if the humerus were extended. Due to its location M. pectoralis superficialis would flex the humerus. This is the only muscle which could act as a flexor on the humerus and not counteract a downward movement of the wing. The only muscles that can act as extensors are the weak Mm. deltoid minor and coracobrachialis anterior. Photographs (Aymar, op. cit.; Queeny, op. cit.; and Storer, op. cit.) also reveal that forward motion is imparted to the bird by a downward and forward movement of the wing, not by a backward push. The tendinous slips are given off by this muscle, one to the region of M. tensor patagialis brevis, the other to the skin.

M. SUPRACORACOIDEUS
(pectoralis secundus of Shufeldt)

Origin.—Fleshy from the median ventral and anterior parts of the sternum, from the portion not occupied by M. pectoralis superficialis and M. coracobrachialis posterior, from the dorsal one-half of the keel, and from the sternal part of the ventral margin of the coracoid, and from the membrane between the sternum and furcula. The largest area of attachment is on the sternal plate.

Insertion.—Tendinous, by a stout tendon on the anconal surface of the external tuberosity of the humerus.

Function.—Elevates the wing and elevates the anterior side of the wing.

Description.—The fibers of this muscle, the second largest flight muscle in the birds examined, gradually converge to form a tendon which passes through the triosseal canal and inserts on the humerus.

Discussion.—The most extensive development of this muscle occurs in small forms having a flapping flight.

M. CORACOBRACHIALIS POSTERIOR
(pectoralis tertius of Shufeldt)

Origin.—Fleshy from the anterior lateral margin of the sternum occupying that part not covered by M. supracoracoideus, and from the distal lateral portion of the coracoid.

Insertion.—Tendinous on the anconal surface of the internal tuberosity of the humerus.

Function.—Depresses humerus, rotates humerus elevating anterior edge of that bone.

Description.—The fusiform contour of this muscle blends with that of M. supracoracoideus and the two appear superficially as one muscle mass.

Discussion.—Shufeldt (op. cit., p. 76) states that "this muscle assists the pectoralis secundus in elevating the humerus when it is brought into action by the contraction of its fibers." That action is not possible in those species described in this paper, and it is difficult to understand how such action is possible in the Raven. Relatively large size of M. coracobrachialis posterior is correlated with increased ability to flap the wing.

M. CORACOBRACHIALIS ANTERIOR
(coraco-humeralis of Shufeldt)

Origin.—Fleshy from the head of the coracoid (see figure 6).

Insertion.—Fleshy on the anterior palmar border of the head of the humerus.

Function.—Acts with M. deltoid minor in extending humerus, depressing anterior edge of humerus.

Description.—Fibers at the posterior proximal border of this muscle blend with those of M. deltoid minor (see M. deltoid minor, description).

Discussion.—See M. deltoid minor.

M. SUBCORACOIDEUS
(coraco-brachialis of Shufeldt)

Origin.—Fleshy, from the dorsal internal side of the coracoid, in the Cardinal extending from internal distal angle to the sterno coracoidal process of the coracoid, and in the other species examined extending from the sternocoracoidal impression of the coracoid almost to the procoracoid.

Insertion.—Tendinous on the internal tuberosity of the humerus anterior to the insertion of corabrachialis posterior.

Function.—Depresses humerus, depresses the posterior edge of the wing, moves the humerus posteriorly.

Description.—In these species M. subcoracoideus is a strong fusiform muscle, well-developed and slightly smaller than M. coracobrachialis posterior.

Discussion.—The increased development of this muscle is probably correlated with flapping flight as it is of importance in depressing the posterior edge of the wing. It is difficult, thus, to explain its reduction in the woodpeckers (Burt, op. cit., p. 489). Howell (1937, p. 370) places this muscle in the axillary matrix of the shoulder group on the basis of its innervation which he found to be in close topographical relationship with the nerve to M. dorsalis scapulae. The innervation as demonstrated in the Cardinal and the White-throated Sparrow indicates that M. subcoracoideus is a part of the ventral division, as its innervation in those two species is by a branch of the nerve supplying M. supracoracoideus.

PART III. ELBOW DERIVATIVES

M. BRACHIALIS

Origin.—Fleshy from the brachial depression of the humerus.
Insertion.—Fleshy on the ulna, between the heads of M. flexor digitorum profundus.
Function.—Flexes forearm, depresses leading edge of forearm.

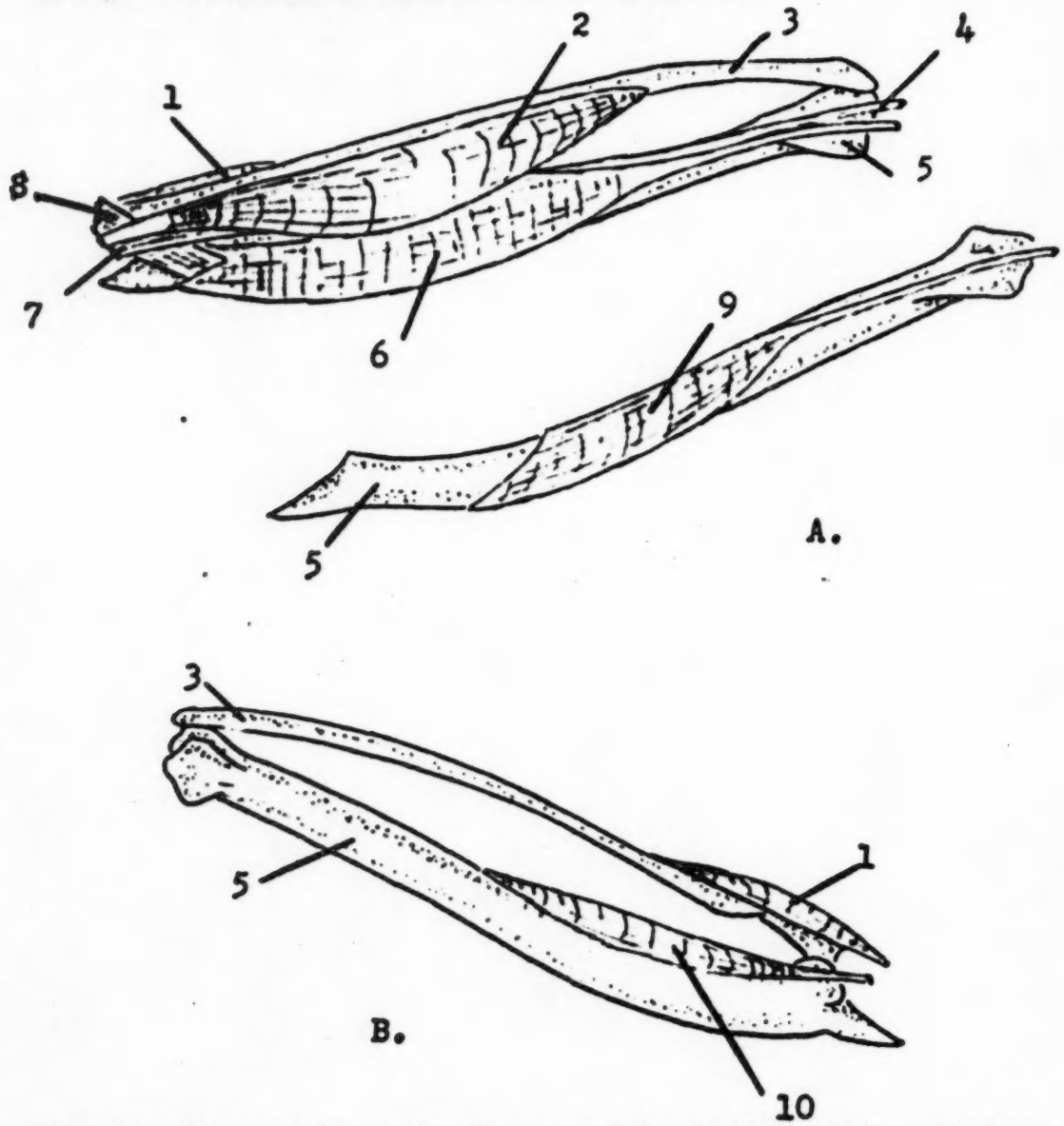


Fig. 10.—Deep muscles of the forearm and hand of *Zonotrichia albicollis.*—A. Palmar view; B. Anconal view. 1. M. supinator brevis; 2. M. pronator longus; 3. radius; 4. M. flexor carpi ulnaris brevis; 5. ulna; 6. M. flexor digitorum profundus; 7. M. pronator brevis; 8. M. brachialis; 9. M. flexor carpi ulnaris; 10. M. anconeus.

Description.—M. brachialis is a short, wide band-like muscle extending posterodorsally from the humerus to the ulna.

Discussion.—No appreciable difference was noted.

M. BICEPS

Origin.—Fleshy from the bicipital surface of the humerus and tendinous from the head of the coracoid above the furcular facet.

Insertion.—Tendinous on the proximal radial surface of the shaft of the ulna (see illustration).

Function.—Flexes the forearm.

Description.—The biceps is less bulky than M. triceps or M. deltoid major. The only evidence of the two headed condition was noted in the originating tendons which united into one tendinous sheet at the proximal margin of the bicipital surface of the humerus.

Discussion.—No appreciable variations of this muscle were noted.

MUSCLES OF THE PATAGIUM

M. DERMO-TENSOR PATAGII

The many variations of this muscle and the two succeeding ones have been noted by several authors and are considered to be of major importance in taxonomy. Shufeldt (op. cit., pp. 105-116) noted two major differences in the insertion of M. dermo-tensor patagii in the passerines. In the Icteridae and Corvidae he found that the tendon of the muscle inserted on the tendon M. tensor patagialis longus. In the Purple Martin the tendon of the dermo-tensor patagii did not join that of tensor patagialis longus but remained distinct to the carpus. In the White-throated Sparrow, English Sparrow, Cardinal, and Song Sparrow the following condition was noted: M. dermo-tensor patagii is formed in the skin of the patagium immediately anterior to M. tensor patagialis longus. The tendon of the dermal muscle apparently joins that of patagialis longus a few millimeters (3-4 mm. in the smaller birds, 6 mm. in the Cardinal) from the belly of the latter. In both preserved and fresh material it was possible to dissect the tendon of M. dermo-tensor patagii to its insertion. It is enclosed in a common sheath with the tendon of tensor patagialis longus, although superficial examination indicates that the tendon of the dermal muscle becomes indistinguishable after juncture with tensor patagialis longus. The tendon of the latter becomes broad and fan-shaped over the distal end of the ulna and divides anterior to the tendon of M. extensor metacarpis radialis. The dorsal division inserts on the base of the process of metacarpal I of the carpometacarpus, the palmar division inserts near the anterior end of the piciform process on the palmar side of the process of metacarpal I. The tendon of dermo-tensor patagii blends into the integument over the leading edge of the hand.

M. TENSOR PATAGIALIS LONGUS

Origin.—Fleshy on the furcula immediately proximal to the insertion of M. tensor patagialis brevis.

Insertion.—Tendinous by two heads, one on the palmar, the other on the dorsal surface of the process of metacarpal I (see figures 4 and 5).

Function.—Maintains position of patagium, aids in flexion of forearm and extension of hand. Contraction of this muscle when the forearm and hand are held in position by more powerful muscles tightens the patagium.

Description.—The tendon of this muscle is flat throughout its length, broad at its origin and narrowing toward its insertion (see M. dermo-tenror patagii).

Discussion.—The insertion of this muscle as observed in these birds agrees with that noted for the hawks and owls by Shufeldt (op. cit.) and the woodpeckers by Burt (op. cit., p. 490), but does not agree with the insertion as described by Shufeldt (op. cit., p. 115) for the Raven.

M. TENSOR PATAGIALIS BREVIS

Origin.—Fleshy on the furcula immediately distal to the origin of tensor patagialis longus.

Insertion.—Tendinous on the ectipicondylar prominence of the humerus, anconal and posterior to the tendinous origin of M. extensor metacarpi radialis.

Function.—Flexes forearm, aids M. extensor metacarpi radialis in extending the hand.

Description.—The tendon of M. tensor patagialis brevis meets the belly of M. extensor metacarpi radialis slightly posterior to the midpoint of the anterior margin of the latter muscle. Here the tendon of the patagial muscle bifurcates, one division inserting

as described, passing over the surface of the extensor muscle, the other joining the fibers which eventually form the tendinous origin of M. extensor metacarpi radialis.

Discussion.—In species that have a more powerful development of M. tensor patagialis brevis flapping flight is facilitated, as this muscle aids in flexing the forearm. In the fringillids and ploceid examined this muscle is of relatively large size and powerful build (see figs. 4 and 8).

MUSCLES OF THE FOREARM AND HAND

M. EXTENSOR METACARPI RADIALIS
(extensor metacarpi radialis longus of Shufeldt)

Origin.—Tendinous from the ectepicondyle of the humerus and fleshy from the area extending from the ectepicondyle of the humerus to the longitudinal midline of the anterior margin of the humerus.

Insertion.—Tendinous by a strong tendon on the process of metacarpal one.

Function.—Extends the hand, flexes forearm.

Description.—The two originating heads are separate for about one-half the length of the belly of the muscle in the Cardinal and for a much lesser length in the smaller birds.

Discussion.—Development of this muscle is correlated with flapping flight, a powerful muscle aiding in extending the hand or in flexing the forearm. In these species M. extensor metacarpi radialis is the largest muscle of the forearm.

M. EXTENSOR DIGITORUM COMMUNIS

Origin.—Tendinous from the ectepicondyle of the humerus.

Insertion.—Tendinous on the proximal anterior dorsal margin of the phalanx I, digit II, and tendinous on the pollex.

Function.—Flexes the forearm, flexes the pollicis and draws it anconally, and extends digit II, also "acting as a tendon the muscle functions as an automatic extensor of the manus when the forearm is extended." (Fisher, op. cit., p. 593.)

Description.—The fibers of this muscle form a tendon which passes anterior to the external condyle of the ulna then proceeds to the anconal process of the ulnare. This tendon then traverses anteriorly over the dorsal surface of metacarpal III to the base of the pollex where the tendon forks. One fork enters the tendinal groove of metacarpal II and terminates on phalanx I, digit II. The other fork, the lesser of the two, inserts on the proximal dorsal surface of the pollex.

Discussion.—If the actions of flexing and extending performed by this muscle is offset by the action of antagonistic and synergistic muscles, its contraction will affect an elevation of the forearm (as may also occur with Mm. flexor metacarpi radialis, supinator brevis, and anconeus).

M. SUPINATOR BREVIS

Origin.—Tendinous, by a long delicate tendon from the anterior surface of the ectepicondyle of the humerus.

Insertion.—Fleshy, on the proximal quarter of the anterior margin of the radius.

Function.—Supinates the forearm, flexes the forearm.

Description.—A minute muscle which is completely hidden by overlying muscles.

Discussion.—The muscles which pronate the forearm are much larger than the corresponding supinators. On the downbeat of the wing the greatest pressure develops on the anterior palmar surface of the wing. Selection would favor development of powerful muscles which would hold the wing firm against this upward force. In flight the inner wing is held with the leading edge higher than the trailing edge. This is accomplished through the action of Mm. deltoid major, deltoid minor, latissimus dorsi, coracobrachialis posterior, and subcoracoideus on the humerus, and Mm. supinator brevis and brachialis on the forearm. Opposing this, the only muscles which would depress the leading edge of the humerus are Mm. proscapulohumeralis and proscapulohumeralis brevis. The hand and part of the forearm with their attached feathers act as a propelling agent and move in level flight with the leading edge lower than the trailing edge. Part of this angle of attack is due to the structure of the feathers and their action in the air stream, but part is determined by muscular control (see Mm. pronator brevis and pronator longus).

M. FLEXOR METACARPA RADIALIS

Origin.—Tendinous, by two tendons which merge at the proximal anconal margin of the ulna. One tendon arises on the humerus distal to the ectepicondylar prominence, posteroventral to the origin of M. extensor digiti communis, and the other arises from the posterior margin of the ulna immediately distal to the olecranon process.

Insertion.—Tendinous, on the intermetacarpal tuberosity of metacarpal II.

Function.—Flexes the hand, aids in flexing the forearm.

Description.—A slim fusiform muscle (see M. supinator brevis).

Discussion.—See muscle supinator brevis.

M. PRONATOR BREVIS

Origin.—Tendinous from an area proximal to the entepicondylar prominence of the humerus.

Insertion.—Fleshy on the middle one-third of the palmar surface of the shaft of the radius.

Function.—Pronates the forearm, flexes the forearm.

Description.—This and the following muscle are among the largest and most prominent of the forearm.

Discussion.—Fisher (op. cit., p. 594), speaking of the Cathartidae, writes: "Although the insertion makes possible the depression of the anterior edge of the wing, in soaring and gliding flight little use need be made of this action. Air pushing upward on the lever arm provided by the long secondaries constantly tends to rotate the anconal surface of the wing anteriorly. M. pronator brevis is of more importance in flexing the forearm." If interpretations of photographs of birds in flapping flight are correct then as J. H. Storer (op. cit., p. 33) observes, "The inner halves move very little during the wing beat and never lose their slope upward to the front." In this case the largest amount of pressure is built up under the anterior portions of the wing, and the lift is greatest over the anterior portions of the wing. Powerful development of those muscles which counteracts this force, those which would aid in depression of the distal portion of the leading edge of the wing, favors flapping flight. This appears to be true in those species examined which have a flapping type flight. Although Storer's observations were made primarily on the large flying birds, such as herons and storks, the basic principles of flight apply to all species. Due to the rapidity of wing beat in the smaller birds, more of the wing functions as a propeller. As the speed of the airstream increases so does the lift on the airfoil. In a fast wing beat the propelling portion of the wing supplies a greater amount of support than in a slow wing beat (even in the large slow flapping species the outer primaries provide some support). In the fast wing beats of the small birds more of the wing is devoted to the propelling-supporting role and less is strictly supporting. The reduction in area of the inner wing, the increase in size and power of the musculature which controls depression and elevation of the wing margins (essential in the propeller stroke) is evident in these small birds and is apparently correlated with this type of wing action.

M. PRONATOR LONGUS

Origin.—Tendinous from an area immediately proximal to the entepicondylar prominence, and fleshy from an area dorsal to this.

Insertion.—This muscle has a large belly which converges into a tendinous sheet that inserts with M. pronator brevis at the latter's extreme distal margin of insertion.

Function.—Pronates the forearm.

Description.—Although careful dissection reveals a separate insertion for this muscle, it blends with M. pronator brevis and in all probability the two muscles function as one.

Discussion.—See M. pronator brevis.

M. EXTENSOR POLLICIS LONGUS
(extensor ossis metacarpi pollicis of Shufeldt)

Origin.—Fleshy from the proximal anconal surface of the shaft of the ulna. This origin is restricted near the proximal radial depression and is in intimate relationship with M. anconeus.

Insertion.—Tendinous on the distal dorsal margin of the tendon of M. extensor metacarpi radialis.

Function.—Aids in the extension of the manus.

Description.—A minute muscle, the smallest of the entire forearm musculature, whose tendon is of hair-like dimensions.

Discussion.—This muscle is of small size in all birds having a flapping flight.

M. ANCONEUS

Origin.—Tendinous from the ectepicondyle of the humerus by a short, flat tendon.

Insertion.—Fleshy on the radial side of the shaft of the ulna.

Function.—Flexes forearm, pronates forearm.

Description.—A flat muscle, the bulk of which lies on the radial side of the ulna. This muscle is small in proportion to others (save the preceding) situated on the forearm.

Discussion.—Fisher (op. cit., p. 620) states: "Mm. pronator longus, pronator brevis and anconeus function to depress the leading edge of the forearm." This is true in the fringillids and ploceid examined as well as in the vultures.

M. EXTENSOR INDICIS LONGUS

Origin.—Fleshy along the ulnar side of the proximal part of the shaft of the radius. The origin covers an area from the articulating head of the radius extending to slightly less than half the length of the radius.

Insertion.—Tendinous on the proximal anterior dorsal surface of the distal phalanx of digit II.

Function.—Extends digit II, aids in extension of the manus.

Description.—Fibers of this elongated muscle converge to form a tendon at about the distal quarter length of the radius. This tendon continues across the anconal surface of metacarpal II and over the leading edge of the proximal phalanx of digit II.

Discussion.—No appreciable difference was noted.

M. FLEXOR DIGITORUM PROFUNDUS

Origin.—Fleshy from the ulna by two heads, one from the posterior margin of the ulna, and the other from the radial side of the ulna (see illustrations).

Insertions.—Tendinous on the proximal anterior palmar surface of phalanx II, digit II.

Function.—Extends carpometacarpus, extends digit II, depresses digit II. The prime function of this muscle is as a depressor of digit II.

Description.—The long tendon of this muscle passes anterior to the pisiform process of the carpometacarpus and from there advances to the anterior margin of metacarpal II, where it is joined by the tendon from M. flexor carpi ulnaris. The tendon progresses over the proximal phalanx of digit II and inserts as noted above.

Discussion.—This muscle and others which insert on the hand and originated on the radius or ulna did not differ appreciably in any of the species reviewed. Fisher (op. cit.) noted a correlation between soaring flight and increased development of these muscles. Whether such a correlation exists in birds having flapping flight cannot be answered on the basis of the examination of the species described herein.

M. FLEXOR CARPI ULNARIS

Origin.—Anterior muscle—tendinous from the entepicondylar prominence. Posterior muscle—tendinous from the same prominence by a tendon which passes through the humero-ulnar pulley.

Insertion.—Anterior muscle—tendinous on the proximal anterior surface of phalanx I, digit II. Posterior muscle—tendinous on the palmar surface of the ulnare.

Function.—Anterior muscle—extends digit II. Posterior muscle—flexes hand.

Description.—The smaller and more anterior muscle lies along the belly of the posterior muscle and the two are covered by a common fascia. The anterior muscle becomes tendinous near the midpoint of length of the ulna. This tendon passes posterior to the pisiform process of the carpometacarpus and proceeds across the dorsal surface of metacarpal II, where it is enclosed in a common sheath with the tendon of M. flexor digitorum profundus to the insertion. The posterior muscle, the larger of the two, becomes tendinous near the distal one-third of the ulna, and this stout tendon inserts as described. Because of the ligamentous connections of the ulnare to the carpometacarpus, contraction of the posterior muscle results in flexion of the hand. The double muscle condition was easily detected in both fresh and preserved material in all four species studied. Except for the covering fascia and a very few fibers exchanged between the bellies of the mus-

cles, they remain separate and distinct. Shufeldt (op. cit., p. 144) found the M. flexor carpi ulnaris to be one muscle. He says: "When we come to examine it carefully in the Raven, especially the distinctness of its external head, and a median fascia that runs longitudinally through its belly, and finally its distal tendinous offshoot, it is not difficult for us to imagine that the muscle originally was composed of two parts, or perhaps two distinct muscles (figs. 31 and 36)." Burt (op. cit., p. 496) found the two-muscle condition in the woodpeckers as did Fisher (op. cit., p. 598) in the Cathartidae.

Discussion.—The development of the two-muscle condition does not seem to be correlated with flight patterns. The relatively large size of M. flexor carpi ulnaris in the fringillids and the ploceid examined as compared with that muscle's development in birds with soaring and gliding flight habits indicates that its size and development are correlated with flapping flight. Greater development of this muscle would result in an increased ability to flex the hand, a factor important in flapping flight.

M. FLEXOR CARPI ULNARIS BREVIS

Origin.—Fleshy from the palmar surface of the shaft of the ulna.

Insertion.—Tendinous near the anterior carpal fossa of metacarpal I of the carpometacarpus.

Function.—Flexes hand, depresses leading edge of the wing.

Description.—M. flexor carpi ulnaris brevis has less volume than the overlying M. flexor digitorum profundus which it resembles in general shape.

Discussion.—Fisher (op. cit., p. 599) states: "Judging from relative size alone, development of the muscle may be correlated with the ability to flap. However, as indicated above, this muscle is important in both flapping and soaring flight because it produces movements vital to both types of flight. Hence no correlation with type of flight is possible."

INTRINSIC MUSCLES OF THE HAND

M. ABDUCTOR POLLICIS
(extensor propius pollicis of Shufeldt)

Origin.—Fleshy from the tendon of M. extensor metacarpi radialis longus just prior to that muscle's insertion.

Insertion.—Mixed fleshy and tendinous midway up the palmar surface of the pollicis.

Function.—Abducts and depresses the pollex.

Description.—See M. adductor pollicis. M. abductor pollicis is longer and more slender than is M. adductor pollicis.

Discussion.—No appreciable variation was noted.

M. ADDUCTOR POLLICIS
(flexor brevis pollicis of Shufeldt)

Origin.—Fleshy from the carpometacarpus (metacarpal II) immediately distal to the base of the pollical facet.

Insertion.—Fleshy on the posterior margin of the pollex.

Function.—Adducts the pollex.

Description.—This is a small thick muscle almost hidden on the posterior side of the pollex.

Discussion.—The pollex is extended by M. abductor pollicis acting independently or as a tendon of M. extensor metacarpi radialis. The pollex is held next to the anterior edge of the wing by Mm. extensor digitorum communis and adductor pollicis.

M. FLEXOR DIGITI III

Origin.—Fleshy from the proximal posterior palmar part of metacarpal III and extending distal half the length of that metacarpal.

Insertion.—Tendinous on the proximal edge of digit III.

Function.—Flexes digit III and as that phalanx is intimately connected with digit II, also flexes digit II.

Description.—This muscle is long and flat lying close to the posterior metacarpal of the carpometacarpus.

Discussion.—No appreciable variation was noted.

M. INTEROSSEUS DORSALIS

Origin.—Fleshy, from the proximal surfaces bounding the intermetacarpal space of metacarpals II and III, and occupying the dorsal proximal portion of that space.

TABLE 2.—Occurrence of muscles of the hand. (Dotted line indicates absence of a muscle.)

MUSCLES OF THE POLLEX

Function	Cathartidae (Fisher, 1946)	Picidae (Burt, 1930)	Corvidae (Shufeldt, 1890)	Fringillidae
Extensors	Abductor pollicis extensor pollicis brevis	abductor pollicis	abductor pollicis	abductor pollicis .....
Flexors	extensor digitorum communis abductor pollicis flexor pollicis	extensor digitorum communis adductor pollicis	extensor digitorum communis adductor pollicis	extensor digitorum communis adductor pollicis .....
Depressors	abductor pollicis flexor pollicis	abductor pollicis	abductor pollicis	abductor pollicis .....
Elevator	extensor pollicis brevis	.....	.....	.....

MUSCLES OF DIGITS II AND III

Function	Cathartidae (Fisher, 1946)	Picidae (Burt, 1930)	Corvidae (Shufeldt, 1890)	Fringillidae
Extensors	extensor digitorum communis extensor indicis longus flexor digitorum profundus interosseus dorsalis abductor indicis abductor indicis brevis	extensor digitorum communis extensor indicis longus flexor digitorum profundus ..... abductor indicis	extensor digitorum communis extensor indicis longus flexor digitorum profundus interosseus dorsalis	extensor digitorum communis extensor indicis longus flexor digitorum profundus interosseus dorsalis ....
Flexors	flexor digiti III *flexor brevis digiti III interosesus palmaris	flexor digiti III flexor brevis digiti III interosseus palmaris	flexor digiti III *flexor brevis digiti III interosseus palmaris	flexor digiti III ..... interosseus palmaris
Depressors	flexor digitorum profundus abductor indicis abductor indicis brevis	flexor digitorum profundus abductor indicis	flexor digitorum profundus	flexor digitorum profundus ....
Elevators	flexor metacarpi brevis interosseus dorsalis interosseus palmaris	flexor metacarpi brevis ..... interosseus palmaris	flexor metacarpi brevis interosseus dorsalis interosseus palmaris	..... interosseus palmaris interosseus dorsalis

*Rudimentary.

Insertion.—Tendinous on the anterior dorsal corner of the distal phalanx of digit II.

Function.—Extends phalanx II of digit II, and in coordination with interosseus palmaris elevates that digit.

Description.—This is the smaller and more delicate of the two interosseus muscles and its tendon is longer and more minute. The muscle is absent in the woodpeckers (Burt, op. cit.).

M. INTEROSSEUS PALMARIS

Origin.—Fleshy from the entire proximal and medial portions of the surfaces of metacarpal II and III bounding the intermetacarpal space. This muscle is located palmar to M. interosseus dorsalis but situated in a similar position and its origin is more extensive than that of interosseus dorsalis.

Insertion.—By a stout tendon to the posterior proximal anconal corner of phalanx II, digit II.

Function.—Flexes phalanx II of digit II, acts in conjunction with M. interosseus dorsalis in elevating digit II.

Description.—The largest interosseus muscle.

Discussion.—The same muscular control of the pollex was noted in the Raven and the four species discussed in this study. In these four species there was no trace of Mm. abductor digiti II, flexor brevis digiti III, and flexor metacarpi brevis, all of which were evident in the Raven (Shufeldt, op. cit.). Flexor brevis digiti III and abductor digiti II are reduced to almost a ligamentous condition in the Raven, and may be represented in the species of Fringillidae and Ploceidae examined by the ligamentous connections of digit III. M. flexor metacarpi brevis varies greatly in the avian musculature described in the literature. In the Raven it appears to be small and delicate (see table 2). Depression and elevation of the manus are restricted by both structure of the articulating surfaces of the bones and the tendons passing across anconal and palmar surfaces.

CONCLUSIONS

The wing myology of the English Sparrow, Cardinal, White-throated Sparrow, and Song Sparrow was found to be essentially similar. Forty-three different muscles controlling the wing were noted in each of the four species. Because of the condition of some of the preserved specimens and the minute size of some of the musculature, no series of volumetric measurements could be made; however, the volumetric measurements which were made, as well as general observations, indicated no appreciable variations in size of the same muscle in each species studied. It appears that in relation to body size, the Song Sparrow had, in general, the least powerful musculature of the four species. There was more similarity of musculature between the Song Sparrow and the White-throated Sparrow than between those species and the Cardinal.

Concerning the muscles which were most variable, either among these four species or between these four species and others described in the literature, the English Sparrow agreed more closely with the White-throated and Song sparrows in detail, although not differing fundamentally from the Cardinal.

Mm. serratus posterior, superficial layer; serratus anterior; serratus profundus; rhomboideus superficialis; rhomboideus profundus; and latissimus dorsi; all differ in extent of origin in these species. No correlation between this and the flight patterns of birds was noted, and only examinations of a larger number of individuals and species could determine if a phylogenetic basis exists for this variation.

The innervations of the muscles of the shoulder were fundamentally similar in all the three fringillids, differing some in detail, however, In the Song Sparrow, White-throated Sparrow, and English Sparrow the innervation for the serratus muscles was by nerves from the eleventh spinal nerve, the first nerve of the brachial plexus. In the Cardinal, however, the innervation of

M. serratus posterior arose from spinal nerve 12, the second nerve of the brachial plexus and the innervation of Mm. serratus profundus and serratus anterior arose from nerve 11. Each bird examined had slight individual variations in structure of the brachial plexus. In several instances two separate nerves were easily distinguished, from their juncture with a spinal nerve to their entrance into muscle tissue, while in other instances the separation of these two nerves was not evident until just before they entered msucle tissue. This was especially noticeable in the two nerves innervating the rhomboideus and serratus muscles of the White-throated Sparrow (see figure 3). The brachial plexus in the fringillids was formed from four trunks, spinal nerves 11, 12, 13, and 14. The branch from nerve 14 was the smallest of the group and did not give rise to any twigs supplying flight muscles, but instead fused with nerve 13.

The brachial plexus of the English Sparrow was formed from three spinal nerves, numbers 11, 12, and 13; no part of spinal nerve 14 joined the plexus.

No differences noted in the wing musculature and innervation of these species appeared to be correlated with sex. The one immature (flying stage) examined did not differ from the adults of the same species in wing myology. Musculature of right and left wings of the same bird did not differ, nor did the innervation of right and left side differ.

Any attempt to correlate relative muscle size and power with flight action must take into consideration wing area, wing loading at any given spot in the beat, and number of wing beats for given unit of time. An examination of the numbers of muscles engaged in a given action as an indication of facility or power of movement is never completely satisfactory, yet it may provide a basis of comparison.

Fisher's work on the Cathartidae provides a source for comparison of musculature of species having an active flapping type of flight and those species which are gliders and soarers, as the latter are described in his publication (Fisher, op. cit.) and the former are considered in this paper. The differences are immediately apparent. Compared with soaring or gliding birds:

(1) In those birds having a flapping flight there is a relative increase in the size and power of the musculature as a whole, and particularly of those muscles which are of importance in the mechanics of flapping flight. There is an increase in size and power (the latter determined both by size and position of origin and insertion) of the following muscles in birds having flapping flight as compared with the same muscles in vultures.

M. serratus posterior
M. serratus anterior
M. deltoid major
M. triceps
M. sternocoracoideus
M. pectoralis superficialis
M. supracoracoideus
M. coracobrachialis posterior
M. subcoracoideus
M. tensor patagialis brevis
M. extensor metacarpi radialis
M. pronator brevis
M. flexor carpi ulnaris

Excluding the muscles the primary function of which is concerned with movements of the hand (see number 2 below), there is an increase in size and power of thirteen muscles, a decrease of size and power in two (Mm. latissimus dorsi and extensor pollicis longus), and comparatively little change in twenty-four muscles.

On the basis of the preceding data there is an increase in facility, scope,

and power of the following movements: Flexion and elevation of the humerus, flexion and extension of the forearm, flexion and extension of the hand, depression and elevation of the wing, especially the former, and depression and elevation on the anterior edge of the wing.

(2) In those birds having a flapping flight there is a reduction in the muscular control of the hand, either through reduction in size and power or through loss of controlling muscles (see table 2). Varied delicate movements of the hand are correlated with the gliding flight and not with the flapping flight.

Some differences in the innervation of the muscles of the shoulder complex were noted and are summarized below.

Cathartidae (after Fisher, 1946)	Fringillidae
M. supracoracoideus A branch from the nerve trunk which distally forms N. brachialis longus.	*M. supracoracoideus* A branch from nerve 12.
M. coracobrachialis posterior A branch of N. brachialis longus inferior.	*M. coracobrachialis posterior* A branch of the nerve which distally forms the nerve supplying the forearm.
M. rhomboideus profundus "A nerve trunk formed by spinal nerves of the posterior cervical region emerges from beneath the anterior edge of M. rhomboideus profundus, and a twig enters the middle of the length of muscle opposite the neck of the scapula." (Fisher, op. cit., p. 582.)	*M. rhomboideus profundus* Branches of spinal nerve 11.
M. subcoracoideus "From the most proximal branch of N. brachialis longus superior. The twig enters the middle of the deep side, and another twig serves M. subscapularis." (M. Fisher, op. cit., p. 587.)	*M. subcoracoideus* A branch of the nerve supplying M. supracoracoideus.

With the complexities of the development of the musculature it is difficult to ascertain what, if any, variations of the musculature may be interpreted as being useful in taxonomy. The development of the patagial muscles and the presence or absence of M. expansor secondarium, and a biceps slip have all been used previously by other authors as aids in determining relationships. The development of Mm. flexor carpi ulnaris, flexor digiti III, flexor brevis digiti III, extensor metacarpi radialis, serratus posterior, latissimus dorsi, and the location and presence or absence of Mm. flexor digiti III, flexor brevis digiti III, interosseus dorsalis, flexor metacarpi brevis, abductor indicis, and abductor indicis brevis may be of additional use in taxonomy.

SUMMARY

The wing myology of three species of Fringillidae and one of Ploceidae were examined. These species were the Cardinal (*Richmondena cardinalis*), the White-throated Sparrow (*Zonotrichia albicollis*), the Song Sparrow (*Melospiza melodia*), and the English Sparrow (*Passer domesticus*).

In each of the above species 43 muscles directly controlling action of the

wing were examined, and the origin and attachment and description of each muscle was noted.

The development of each muscle was compared in the above species, and with the musculature as described by other authors of the new world vultures, the woodpeckers, and the Raven. The function of each muscle was likewise compared.

The following was noted:

The wing myology of the four species examined was essentially similar.

The Song Sparrow relatively had the least powerful musculature.

The innervations of the shoulder musculature was fundamentally similar in the fringillids.

In the fringillids examined the brachial plexus was formed by four spinal nerves. In the one ploceid examined the brachial plexus was formed by three spinal nerves.

Compared with birds having soaring or gliding flight, the species examined had a relative increase in size and power of the musculature, particularly of those muscles which are of importance in flapping flight.

Compared with birds having soaring or gliding flight, the species examined had a reduction in the number and power of muscles controlling movements of the hands.

Thirteen muscles were noted of which the differential development or occurrence might be of taxonomic use.

REFERENCES

AYMAR, G. C. 1935—Bird flight. Dodd, Mead.

BEDDARD, F. E. 1898—The structure and classification of birds. Longmans, Green and Co., London.

BERGER, ANDREW J. 1953—On the locomotor anatomy of the blue coua, *Coua caerulea*. Auk 70(1):49-83.

BURT, W. H. 1930—Adaptive modifications in the woodpeckers. Univ. Calif. Pub. Zool. 32(8):455-524.

CHAMBERLAIN, F. W. 1943—Atlas of avian anatomy. Hallenbeck Printing Company, Lansing, Michigan.

FISHER, H. I. 1946—Adaptations and comparative anatomy of the locomotor apparatus of new world vultures. Amer. Midl. Nat. 35(3):545-724.

FÜRBRINGER, M. 1888—Untersuchungen zur morphologie und Systematik der Vögel zugleich ein Beitrag zur Anatomie der Stütz-und Bewegungsorgane. T. J. van Holkema, Amsterdam.

GRASSE, P., ET AL. 1950—Traite de Zoologie. Masson et Cie, Paris 15:108-118.

HOSKING, E. AND C. NEWBERRY 1949—Birds in action. Collins, St. James' Place, London.

HOWARD, H. 1929—The avifauna of Emeryville Shellmound. Univ. Calif. Publ. Zool. 32:301-394.

HOWELL, A. B. 1937—Morphogenegis of the shoulder architecture: Aves. Auk 54(3):364-375.

QUEENY, E. M. 1947—Prairie wings. J. B. Lippincott Co., New York.

SHUFELDT, R. W. 1890—The myology of the Raven (Corvus corax sinuatus). Macmillan Co., New York.

STORER, J. H. 1948—The flight of birds. Cranbrook Institute of Science. Bulletin No. 28.

STRESEMANN, E. AVES 1927-1934—In Handbuch der Zoologie. Edited by Kükenthal, Walter de Gruyter, Berlin.

Distribution of Californian Mosses

Leo Francis Koch
Bakersfield College, Bakersfield, California

Our previous knowledge of mosses in California largely concerns their taxonomy. Ecology and geography have received little attention probably because the moss flora has long needed a critical re-examination. The author undertook a revision of the Californian mosses, with Grout's (1928-1940) *Moss flora of North America north of Mexico* as a basis, before analyzing their distribution. Three preliminary papers (Koch, 1948, 1949a, 1949b) and an annotated list of 317 species for the state (Koch, 1950a) are the result of that research. Since then, three additional species (Koch, 1950b, 1951a) have been added to the known flora of California, bringing the total to 320 mosses. Very recently two new species, *Fissidens milobakeri* Koch and *Tortula stanfordensis* Steere have been described from California material (Koch, 1951c; Steere, 1951), but these are not incorporated in this paper.

The present paper embodies a classification of the patterns of known distribution of mosses in California, a comparison of these patterns with the units of vegetational areas previously proposed for California, and finally an analysis of world-wide distribution of California mosses based upon a proposed system of plant geography.

ACKNOWLEDGEMENTS

Professor Milo S. Baker of Santa Rosa Junior College, Santa Rosa, California, first aroused the interest of the writer in the study of bryophytes. A scholarship from the New York Botanical Garden, which enabled the author to work on California specimens at that institution during January 1948, is gratefully acknowledged. Helpful suggestions and criticisms from Dr. W. C. Steere during the progress of the investigation are deeply appreciated. The writer is also grateful to the following bryologists for determination of many species of difficult genera: A. L. Andrews, E. B. Bartram, H. S. Conard, Seville Flowers, Geneva Sayre, A. J. Sharp, E. C. Wallace, W. H. Welch, and F. E. Wynne-Hillier. In addition, thanks are due the curators of herbaria at the following institutions for the loan of specimens: California Academy of Sciences, Duke University, New York Botanical Garden, Stanford University, University of California, University of California at Los Angeles, and the University of Michigan. Specimens from the private herbaria of E. B. Bartram and H. S. Conard were also available. Undetermined collections of Californian mosses were generously contributed by the following: D. G. Catcheside, W. B. Cooke, I. M. Haring, G. J. Ikenberry, J. M. Linsdale, E. E. Morse and H. K. Wagnon. Many valuable references to bryological literature were supplied by W C. Steere and E. V. Watson. Miss Annetta Carter, Senior Botanist in the Herbarium of the University of California, was helpful in many ways. Editorial and other assistance was provided by my wife, Shirley Jane Koch.

REVIEW OF LITERATURE

BRYOPHYTES

Lesquereux (1865) first summarized the geographical affinities of the moss flora of California. His analysis clearly indicates the dissimilarity of mosses from eastern and western North America:

"42 peculiar to western North America
42 common to California, eastern North America and Europe
34 common to California and Europe but not eastern North America
00 common to California and eastern North America only
3 anomalous

121 Total"

That a few of the collections cited may be from Arizona or Oregon scarcely detracts from Lesquereux's critical analysis. His theory was that species common to eastern North America, California and Europe are mostly "wandering or universal" species whereas those common only to Europe and California are "typical" forms. He continued: "This . . . shows the relation of the flora to Europe and its entire disruption from that of eastern North America." Lesquereux drew parallels between the experiences of W. H. Brewer on Mount Shasta in California, W. P. Schimper in the Sierra Nevada of Spain, D. de Montperreux in the Caucausus, and French botanists in Algeria. These men noted a paucity of bryophytes there compared to the richer and more varied moss flora of the far north. Lesquereux concluded that, "All of the countries are about on the latitude of California and evidently we can trace to a similarity of mere climatic circumstances the first cause of the extraordinary relation of the bryological vegetation."

Similar conclusions were presented by Howe (1896): "The following interesting table shows that while the hepatic flora of California is more nearly related to that of Central and Northern Europe than to that of *Gray's Manual* region, it is yet more closely related to that of the Mediterranean region.

In common with *Gray's Manual* region	(32) 46%
In common with British Islands	(31) 44%
In common with Central and northern Europe	(36) 51%
In common with the Mediterranean region	(37) 53%
Peculiar to Pacific Coast of Northern America	(22) 31%

Total of 70 species"

Howe (1898) repeated these conclusions in different form: "It will be seen that of our 86 species (Hepaticae and Anthocerotes), 37 (43½%) are in the British Isles; 46 (53½%) in northern and central Europe; 36 (42%) in northern Asia; and 37 (43½%) are peculiar to the Pacific slope of America, several of them having not yet been found outside of California. It is of some interest to remark that the number of species peculiar to the Pacific slope is proportionately greater than those peculiar to the *Gray's Manual* region, even though we may not stop to prove this by figures. The difference between 43% and 53½% is sufficient to justify the assertion that the hepatic flora of California has more in common with Europe than with the eastern and central United States."

Herzog (1926) compiled the only comprehensive system of unit areas based on the distribution of bryophytes. He defined a "Nordamerikanisches Vegetationsreich" within which he considered the "pazifische Waldgebiet" including the Rocky Mountains, as a separate district. Most of California was included in a "Südliche Abschnitt" of his Pacific district although the southern desert areas were mentioned as "Übergangsgebiete" to the central American tropics. Undoubtedly, information about geography, and data about bryophyte specimens available to him were insufficient to indicate the botanical diversity west of the Rocky Mountains.

HIGHER PLANTS

Abrams (1925) summarized the major geographical affinities of the higher plants of California as follows: (1) the flora of the higher mountains is boreal in origin, made up chiefly of genera common to northern North America and Eurasia. (2) the flora of the deserts is largely of Mexican origin.

(3) the flora of cismontane California is composed of both these groups together with many endemics and relics.

Campbell and Wiggins (1947) analyzed the world-wide distribution of higher plants in considerable detail. They concluded that "relict" species, like the redwoods and cypresses, perhaps represent the late Mesozoic flora that had developed before the complete isolation of the area; cosmopolitan genera such as *Acer*, *Populus*, *Quercus*, and *Salix*, probably reached California from the north via the Coast Ranges and the Sierra Nevada. The Cactaceae and some genera which occur in California, Chile and Mexico, they said, are undoubtedly of southern origin. They include a table of geographical distribution of higher plants in California.

Jepson (1925) stated that 1416 (about 40%) of the 3727 native species of ferns and seed plants of California are endemic. To my knowledge, Jepson is the only botanist who defined a series of separate and distinct areas correlated with the distribution of endemic plants in California. His areas are: (1) Low Foothill Area, 100-1500 or 3000 feet altitude; (2) Tehaman Area, 3000-7000 feet altitude; (3) Tehachapan Area, the San Bernardino Mountains, San Gabriel Mountains to Mount Pinos and Frazier Mountain, and the Tehachapi Mountains to the southern Sierra Nevada in Kern and Tulare counties; (4) Mohavan Area, almost coextensive with the Mohave Desert; (5) Death Valley; (6) Klamath Area, a northwestern section of coniferous forest; (7) Napa-Lake Area, 800-3000 feet altitude, including the lower mountains of Napa and Lake counties; (8) Lucian Area, the Santa Lucia Mountains overhanging the Pacific Ocean; (9) Santa Barbara Insular Area; and (10) Franciscan Area, a coastal belt from northern Monterey County northward to southern Mendocino County.

CONCEPTS AND METHODOLOGY IN PLANT GEOGRAPHY

Any synthesis of knowledge involves the derivation of practical concepts of basic units as well as the development of systems for classifying them. Plant geographers have not been markedly successful in attaining agreement on either of these objectives. Each investigator has had to choose and define terminology and methodology.

The basic unit of plant geography, in its broadest sense, may be defined as follows: A floral unit is a group of taxonomic entities having a basically similar pattern of distribution, essentially equivalent ecological characteristics, and a common migrational history.

The usual analysis of a flora involves sorting the species on too broad a basis into groups which are termed "elements," which are not the same as the writer's "floral unit," because they are loosely used and frequently subdivided. A floral element, floristic element, and a phytogeographical element are apparently the same. The simplest term "floral" as used by Wulff (1943) seems preferable. Different investigators have derived elements by applying different concepts and methods. The unlike elements and their dissimilar nomenclature necessarily increase the difficulty of correlating the results of different investigations.

Areschoug and Christ, independently in 1867, used the term "element" in a purely geographical sense (Wulff, 1943). Braun-Blanquet advocated this usage and defined the floral element as the floristic and phytosociologic expres-

sion of a territory of limited extent (Cain, 1944). Braun-Blanquet's nomenclature is entirely geographical.

Other workers, for example Amann (1928), employed ecological concepts also. Amann's nomenclatural system is derived from a mixture of ecology and geography. Several of his terms are: "central-européen, meridional-euro péen, boreal et subarctique-alpin," and "alpin proprement dit."

Later students introduced historical qualifications into their concepts of a floral element. For instance, Sharsmith (1945) referring to the flora of Mt. Hamilton Range, California stated: "Like all other floras, it is composed of diverse floristic elements (groups of species), each homogeneous in that it has had a common center of origin and dispersal from which the component species migrated. These elements arose in response to certain physical and biological factors, and the species within each element have a similar migrational history and a basically similar pattern of distribution."

Wulff (1943) analyzed concepts of floral elements and concluded that the species in any flora may be subdivided according to any one of five different "principles." The division of a flora into groups of species when applying one of Wulff's principles yields one series of floral elements. In this way, Wulff derived five series of floral "elements": geographical, ecological, genetic, migrational, and historical. In this system, each species in a flora could belong to five different kinds of elements simultaneously.

Cain (1944) approved the conclusions of Wulff and suggested the usage of the term "element" in its widest variety of applications.

Chaney (1944) analyzing fossil floras of Pliocene age, stated: "An element may be defined as a group of fossil plants whose modern related species occupy a major geographical and climatic province. . . . Each of the elements designated in Tertiary floras may be further subdivided into components which represent their major floristic units." Later he continued: "It should be emphasized that element and component names are applied to fossil plants to emphasize their resemblance to modern vegetation, and that they do not necessarily coincide with the names of units involved in the study of living plants."

SOME FUNDAMENTAL CONSIDERATIONS

An "element" derived from geographical data alone is essentially a static concept. It is also too heterogeneous a grouping to serve as a basic unit for interpretive plant geography. Two species now having the same geographical distribution may not have equivalent ecological characteristics and so may not react similarly to a change of environment. Present geographically similar distribution may be a coincidence.

The substitution of another "principle" for the geographical one does not solve the difficulty posed by the heterogeneous "element." For instance in her discussion of the Mount Hamilton Range flora, Sharsmith (1945) apparently concluded that a historical factor is more important than present geographical distribution. She recognized a "Sonoran floristic element" and a "Northern floristic element" on the basis of a more remote common region of origin for the species concerned. She described "Great Basin and Desert derivatives" of the "Sonoran floristic element," now largely characteristic of the arid Great Basin. A second group of derivative species of the "Sonoran floristic element" was then noted: "It consists of species which have their centers of distribution in northern Baja California and cismontane southern California,

or which have their affinities in these areas, but which are presumed to have been derived from the "Sonoran floristic element." These two groups of species do not have a "basically similar pattern of distribution," nor can they have had a "common migrational history," both qualifications postulated by Sharsmith for a floral element.

Similarly her "Northern floristic element" has no definite significance for Californian plants. A bipolar, circumboreal, Europe-North American, Asia-North American, or a Pacific Coastal group of species could have entered California from the north. To include groups of species with these diverse ranges in one floral grouping does not contribute much information about the history of floras. A suitable basic unit for interpretive plant geography should be homogeneous in terms of more than one attribute.

Taxonomists, ecologists, and plant geographers are accumulating information about, or investigating phenomena concerned with different basic, botanical units, namely, the species, the plant community, and the floral unit. The underlying difficulty of devising a practical definition for these basic units is embodied in Cooper's (1926) "one fundamental premise, . . . the universality of change."

Geographical and ecological elements as derived by Wulff represent current similarities and differences in plant distribution caused by continuous change in floras of the world. A catalogue of patterns of distribution and habitat preferences of species is one of the ultimate aims of the descriptive phases of plant geography and ecology respectively. If differences in areas of distribution of one species in successive time periods are the result of migration, which in turn is directly related to the ecological character of plants, an account of history and causes of change in floras should deal with a basic unit homogeneous both in its geography and ecology.

Patterns of distribution and plant communities are essentially static concepts. The dynamic processes in terms of which phytogeographers can hope to arrive at a satisfactory concept of a basic unit, and also an explanation of change in floras, are evolution, plant migration, and environmental change. We are not concerned with the physical mechanisms of these processes but with their effect upon floras of the world, either as the appearance of new species, the occurrence of species in new localities, or as the disappearance of species, in successive time periods. Evolution need not be considered further except to note that recognition of genetic continuity between a living plant and its fossil ancestor depends upon acceptance of the theory that heredity is attested by morphological resemblance.

Phytogeographers are primarily concerned with changes in floras correlated with migration and environmental change. Many theories relating to historical plant geography are derived from a comparison of data, from paleobotany and geology with those of taxonomy and geography, concerning a common basic unit, the species. Differences in area occupied by a species population at various times can be considered direct evidence of migration; environmental change may be involved. We cannot discuss migration intelligently without designating the regions from which, and to which, it occurred, or without recording the time it started and ended. The region of origin, the migration route, and the time of arrival in a new area (the basis of Wulff's genetic, migrational, and historical elements respectively) are but three aspects of a

continuous space-time journey including migration if any, evolution, if any, and duration of taxonomic units in successive time periods.

According to Mason (1947), plant migration must be construed as the movement of an interbreeding population, and not as a movement of individuals or floras. He argued that the interbreeding population is the functional unit within the community because it provides the mechanism of continuity, of migration, and of adaptive change. Allowing for some lack of universal applicability in these statements, for they take no account of apomictic and habitually inbreeding species, we may accept the ideas as largely true. Perhaps they would be more nearly correct if we substituted the word "reproducing" for "interbreeding." Mason's line of reasoning can be applied equally well to our concepts of basic units in taxonomy and plant geography. A species concept in terms of reproducing natural populations, provides the dynamic factor for the derivation of a practical basic unit in interpretive plant geography.

In summary, the distributional history of a flora entails a synthesis of three kinds of factual evidence which can be correlated with Wulff's five kinds of elements and portions of the quotation taken from Sharsmith:

Type of evidence	Wulff's elements	Sharsmith
Geographical	"Geographical"	"a basically similar pattern of distribution"
Ecological	"Ecological"	"response to certain physical and biological factors"
Geological	"Genetic, Migrational, Historical"	"a similar migrational history"

To reiterate, the basic, or floral unit of historical plant geography in its broadest sense, is a group of taxonomic entities having a basically similar pattern of distribution, essentially equivalent ecological characteristics, and a common migrational history.

DERIVATION OF FLORAL UNITS

The analysis of fossil floras, developed by Chaney and his students (Chaney, 1944; Axelrod, 1939), has resulted in important contributions to our knowledge of the history of floras of western North America. Their method applies ecological principles and geographical data as well as the facts of paleobotany. Similarly in the study of living floras, phytogeographers should consider all three types of evidence.

A possible method for integrating them would be to divide and subdivide a flora in three successive steps, each involving the application of one of the three criteria (geographical, ecological, and paleobotanical (geological), corresponding to the three principal clauses in our definition of a floral unit. A quotation from Raup (1942) is pertinent: "We would be better advised to base our study of plant geography, and any system of classification for botanical regions upon the existing plant life rather than upon partially hypothetical trends of development. A system 'based on primary facts of observation, . . . provides a more solid basis for scientific work than a system based partially on deduced facts.' (Hartshorne, 1939)"

Ecological principles and the geological record, when compared to geographical distribution are less amenable to direct observation, and are therefore based upon a greater proportion of "deduced facts." The first subdivision

of a flora should be according to geographical evidence, providing a convenient and practical framework for our nomenclatural system.

Continents are practical geographical units because they are universally understood and easily indicated. A group of species having the same distribution in terms of continents is designated a "division" of the flora of the world or any region. These large groupings are useful but must be subdivided according to geographical patterns of plant distribution within continents for the study of smaller areas. The resultant groups of species are designated "elements," thereby conserving the original geographical usage of the term. Divisions and elements can only be significant when determined from the total distribution of each species concerned. Areas characterized by floral elements may not be continuous, nor will they be mutually exclusive.

Synecology deals with the association of organisms in specific habitats. Geographical distribution of plant communities can be correlated, at least partially, with some of the factors in the environment. If plant migration is influenced by the interaction of tolerance, or ecological amplitude of species, and factors in the environment, natural association is an indication of similar ecological responses for plants. If this assumption is right, plant communities are an observable, factual method of classification of species. In comparison, knowledge of fossil floras and other geological evidence is relatively difficult to apply. Ecological evidence in the form of plant communities should be applied in the second step of floral subdivisions. Groups of species within each floral element, which we assume to have equivalent ecological responses because of their association in specific habitats, are designated as "fractions."

Chaney (1944) designated his subdivisions of fossil elements as "components," but the use of his terminology in the study of living floras may lead to confusion. The phrases, identifying Chaney's components, are appropriate models for similar phrases to distinguish floral fractions.

Each floral fraction, supposedly, would react as a unit to any set of environmental factors. If a change of environment included extremes beyond the range of tolerance of the component plants, a migration or extinction of fractions rather than species could logically occur.

Theoretically, fractions comprise one or more units, each of one or more species, whose fossil equivalents had a basically similar geographical distribution and ecological characteristics. Chaney and his coworkers identified fossil equivalents of living species of western North America, presumably from morphological comparison indicating natural relationship. To illustrate, seven plants in Cooper's (1922) "Chaparral Climax" and their fossil equivalents are:

Modern species (Cooper)	Fossil equivalent (Chaney)
Arctostaphylos glauca	*Arctostaphylos preglauca*
Ceanothus cuneatus	*Ceanothus precuneatus*
Cercocarpus betuloides	*Cercocarpus antiquus*
Photinia arbutifolia	*Photinia sonomensis*
Rhamnus crocea	*Rhamnus moragensis*
Rhus integrifolia	*Rhus preintegrifolia*
Rhus laurina	*Rhus prelaurina*

The migrational history of all species in a floral fraction may not be identical because of interference of historical factors such as orogeny, subsidence, or change of climate, or as a result of biological factors. At this point geological evidence of all kinds may be applied in subdividing fractions into floral units.

Floral divisions, elements, fractions and units cannot be compared to the categorical hierarchy of plant taxonomy. The three kinds of evidence (geographical, ecological, and geological) are compiled and applied independently. The scheme is proposed tentatively and its applicability remains to be established.

DISTRIBUTION OF CALIFORNIAN MOSSES

OUTLINE OF FLORAL SUBDIVISIONS ACCORDING TO THREE KINDS OF EVIDENCE

	The Flora of the World	
	Both Hemispheres (????)	
	Northern Hemisphere	
"Divisions"	Three Continents	Continental Occurrence
	Europe-North America	
	Asia-North America	
	North America	
"Elements"	Transcontinental	Patterns of Distribution
	Rocky Mountains	
	Arid Southwest	
	Pacific Slope	
	California and Baja California	
"Fractions"	Desert Scrub ?	Ecological
	Sagebrush ?	
	Redwood ?	
	Montane ?	
	Chaparral ?	
"Units"	*Orthotrichum bolanderi* ??	Geological
	Grimmia hamulosa ??	

WORLD-WIDE GEOGRAPHICAL AFFINITIES

Our knowledge of the geography of mosses in the southern hemisphere is fragmentary compared to that in the boreal regions. Known stations for Californian species in the austral regions are so few that floral divisions cannot be outlined for species common to both hemispheres. The following groups are based upon an attempted correlation of climate with the distribution of species.

IN BOTH HEMISPHERES

	Number of Species	Percentage of Total Flora
Weedy, in all zones	3	0.9
Mountainous and polar regions with cold to temperate climates	57	17.8
Regions with temperate to subtropical climates	17	5.3
Totals	77	24.0

NORTHERN HEMISPHERE ONLY

Floral Divisions	Number of Species	Percentage of Total Flora
Three Boreal Continents	102	31.9
Europe-North America	39	12.2
Asia-North America	5	1.6
North America	93	29.1
Totals	239	74.8
Anomalous species, distribution not corresponding with any of the groups above	4	1.3
Grand Totals	320	100.0

As Lynge (1932) indicated, the phytogeographic disposition of a species can only be based on a knowledge of that entity throughout its range. Knowledge of species in an area the size of California cannot provide data for a valid classification of species widely scattered over several continents. For this reason the groups of species not restricted to North America are not further subdivided. The following tentative elements in the North American Division of the California moss flora are based on the known range of species compiled from available bryological literature.

ELEMENTS OF NORTH AMERICAN DIVISION

	Number of Species	Percentage of Flora
Transcontinental	3	0.9
Rocky Mountain and westward	8	2.5
Southwestern United States and northern Mexico	9	2.9
Pacific slope from Alaska to Baja California	56	17.5
California and northern Baja California	17	5.3
Totals	93	29.1

CALIFORNIAN MOSSES GROUPED ACCORDING TO THEIR KNOWN DISTRIBUTION

The following classification of patterns of distribution of mosses in California is based upon maps of the known stations of 193 mosses. The remaining 127 species reported in California are not included because most of them are known from so few stations in the state that a pattern of distribution cannot be recognized. Exceptions are the three weedy species (*Bryum argentum*, *Bryum capillare*, and *Funaria hygrometrica*) and the "anomalous" group of species (*Fontinalis neomexicana*, *Grimmia torquata*, *Orthodontium pellucens*, and *Vesicularia amphibola*). Complete lists of species in each group, division, or element proposed in the previous section are included in the original thesis (Koch, 1950c). The disposition of each species is necessarily provisional pending more knowledge.

Four major types of distributional patterns in California appear to have a climatic or environmental basis:

(1) Widespread, in the Coast Ranges and in the Sierra Nevada but not in the desert regions of southeastern California or in the Great Basin east of the Sierra Nevada (fig. 1).

(2) Montane, restricted to mountainous areas at more than 3000 feet above sea level (fig. 2).

(3) Coastal, in the counties along the Pacific Ocean (fig. 3).

(4) Desert, largely restricted to the arid southeastern part of California. Isolated stations in exceptionally arid localities farther north may exist (fig. 4).

Known range, in degrees north latitude, in California is arbitrarily used as a criterion for further subdivision. The distributional patterns are listed separately for groups, divisions, and elements in the following account. Until similar studies in other areas have outlined the details of phytogeographical patterns, we can hardly distinguish true floral elements, much less fractions or units.

Floral divisions, elements, fractions and units cannot be compared to the categorical hierarchy of plant taxonomy. The three kinds of evidence (geographical, ecological, and geological) are compiled and applied independently. The scheme is proposed tentatively and its applicability remains to be established.

DISTRIBUTION OF CALIFORNIAN MOSSES

OUTLINE OF FLORAL SUBDIVISIONS ACCORDING TO THREE KINDS OF EVIDENCE

	The Flora of the World	
	Both Hemispheres (????)	
	Northern Hemisphere	
"Divisions"	Three Continents	Continental Occurrence
	Europe-North America	
	Asia-North America	
	North America	
"Elements"	Transcontinental	Patterns of Distribution
	Rocky Mountains	
	Arid Southwest	
	Pacific Slope	
	California and Baja California	
"Fractions"	Desert Scrub ?	Ecological
	Sagebrush ?	
	Redwood ?	
	Montane ?	
	Chaparral ?	
"Units"	*Orthotrichum bolanderi* ??	Geological
	Grimmia hamulosa ??	

WORLD-WIDE GEOGRAPHICAL AFFINITIES

Our knowledge of the geography of mosses in the southern hemisphere is fragmentary compared to that in the boreal regions. Known stations for Californian species in the austral regions are so few that floral divisions cannot be outlined for species common to both hemispheres. The following groups are based upon an attempted correlation of climate with the distribution of species.

IN BOTH HEMISPHERES

	Number of Species	Percentage of Total Flora
Weedy, in all zones	3	0.9
Mountainous and polar regions with cold to temperate climates	57	17.8
Regions with temperate to subtropical climates	17	5.3
Totals	77	24.0

NORTHERN HEMISPHERE ONLY

Floral Divisions	Number of Species	Percentage of Total Flora
Three Boreal Continents	102	31.9
Europe-North America	39	12.2
Asia-North America	5	1.6
North America	93	29.1
Totals	239	74.8
Anomalous species, distribution not corresponding with any of the groups above	4	1.3
Grand Totals	320	100.0

As Lynge (1932) indicated, the phytogeographic disposition of a species can only be based on a knowledge of that entity throughout its range. Knowledge of species in an area the size of California cannot provide data for a valid classification of species widely scattered over several continents. For this reason the groups of species not restricted to North America are not further subdivided. The following tentative elements in the North American Division of the California moss flora are based on the known range of species compiled from available bryological literature.

ELEMENTS OF NORTH AMERICAN DIVISION

	Number of Species	Percentage of Flora
Transcontinental	3	0.9
Rocky Mountain and westward	8	2.5
Southwestern United States and northern Mexico	9	2.9
Pacific slope from Alaska to Baja California	56	17.5
California and northern Baja California	17	5.3
Totals	93	29.1

CALIFORNIAN MOSSES GROUPED ACCORDING TO THEIR KNOWN DISTRIBUTION

The following classification of patterns of distribution of mosses in California is based upon maps of the known stations of 193 mosses. The remaining 127 species reported in California are not included because most of them are known from so few stations in the state that a pattern of distribution cannot be recognized. Exceptions are the three weedy species (*Bryum argentum*, *Bryum capillare*, and *Funaria hygrometrica*) and the "anomalous" group of species (*Fontinalis neomexicana*, *Grimmia torquata*, *Orthodontium pellucens*, and *Vesicularia amphibola*). Complete lists of species in each group, division, or element proposed in the previous section are included in the original thesis (Koch, 1950c). The disposition of each species is necessarily provisional pending more knowledge.

Four major types of distributional patterns in California appear to have a climatic or environmental basis:

(1) Widespread, in the Coast Ranges and in the Sierra Nevada but not in the desert regions of southeastern California or in the Great Basin east of the Sierra Nevada (fig. 1).

(2) Montane, restricted to mountainous areas at more than 3000 feet above sea level (fig. 2).

(3) Coastal, in the counties along the Pacific Ocean (fig. 3).

(4) Desert, largely restricted to the arid southeastern part of California. Isolated stations in exceptionally arid localities farther north may exist (fig. 4).

Known range, in degrees north latitude, in California is arbitrarily used as a criterion for further subdivision. The distributional patterns are listed separately for groups, divisions, and elements in the following account. Until similar studies in other areas have outlined the details of phytogeographical patterns, we can hardly distinguish true floral elements, much less fractions or units.

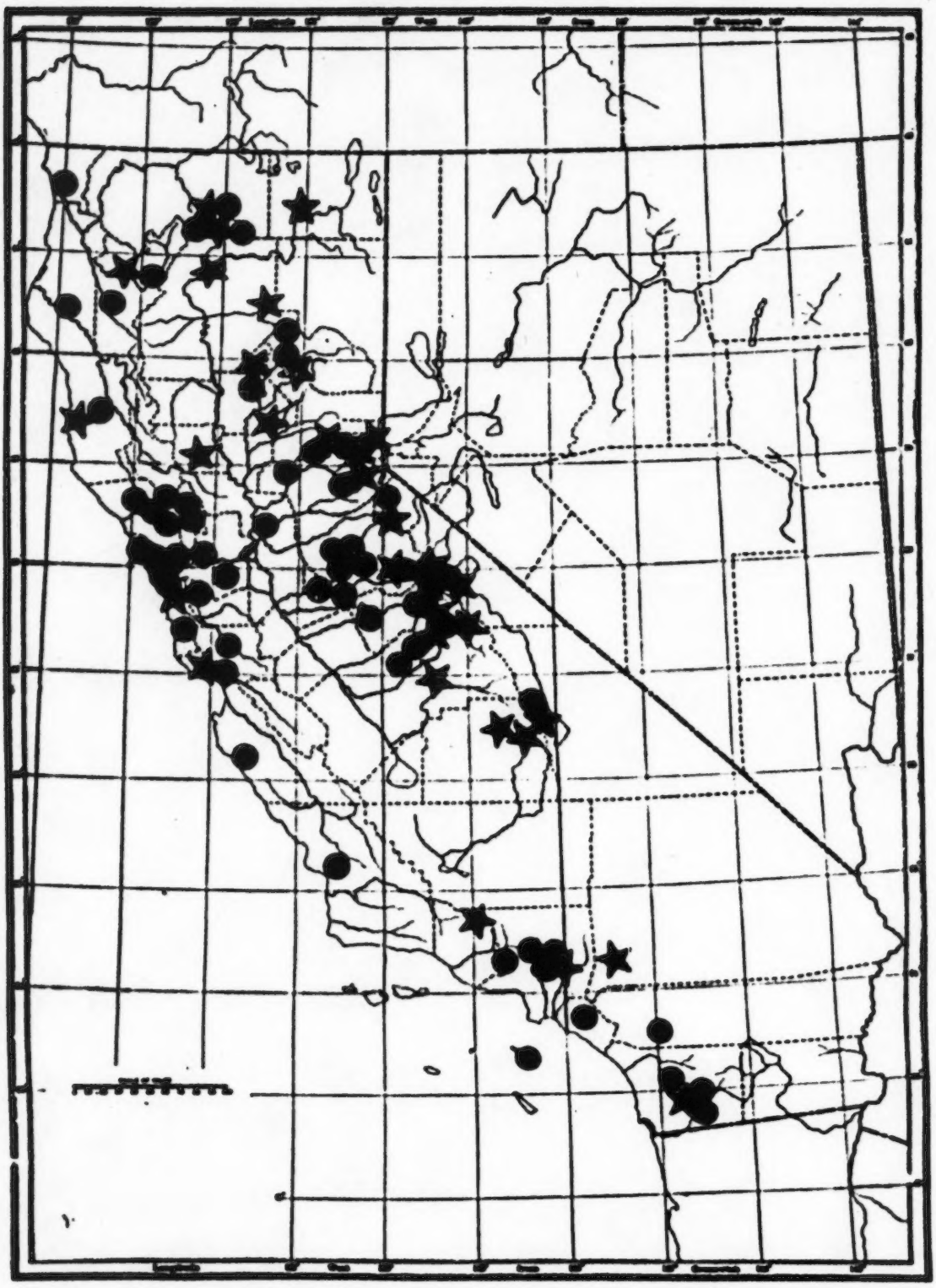


Fig. 1.—Widespread distribution pattern of Californian Mosses, represented by known stations of *Grimmia trichophylla* and *Leptobryum pyriforme*. The former species is represented by dots; the latter by stars.

COLD TO TEMPERATE CLIMATES

Species	Californian Range in Degrees North Latitude	Major Pattern of Distribution in California
Aulacomnium palustre		
Bryum pseudotriquetrum		
Ceratodon purpureus		
Cratoneuron filicinum		

Species	Californian Range in Degrees North Latitude	Major Pattern of Distribution in California
Drepanocladus aduncus		
Encalypta vulgaris		
Fontinalis antipyretica	42-32	Widespread
Grimmia trichophylla		
Leptobryum pyriforme		
Leptodictyum riparium		
Orthotrichum rupestre		
Polytrichum juniperinum		
Polytrichum piliferum		
Tortula ruralis		
Bryum turbinatum		
Drepanocladus exannulatus		
Drepanocladus fluitans	42-36	Widespread
Grimmia apicola		
Grimmia apocarpa		
Pogonatum alpinum		
Rhacomitrum heterostichum		
Encalypta ciliata		
Polytrichum commune	42-37	Widespread
Rhacomitrium aciculare		
Bryum caespiticium		
Plagiothecium denticulatum	42-38	Widespread
Bartramia ithyphylla		
Calliergon stramineum		
Campylium polygamum		
Didymodon recurvirostris		
Distichium capillaceum	42-36	Montane
Drepanocladus uncinatus		
Isopterygium pulchellum		
Meesia triquetra		
Meesia uliginosa		
Pohlia cruda		
Sphagnum fimbriatum		
TEMPERATE TO SUBTROPICAL CLIMATES		
Amblystegium serpens		
Bryum canariense		
Hedwigia ciliata	42-32	Widespread
Leptodictyum trichopodium		
Pterogonium gracile		
Tortula princeps		
Eucladium verticillatum		
Grimmia laevigata		
Grimmia pulvinata	40-32	Widespread
Gymnostomum calcareum		
Weissia controversa		
Tortula muralis	40-32	Coastal
Desmatodon convolutus	38-32	Widespread
THREE BOREAL CONTINENTS DIVISION		
Amblystegium varium		
Anisothecium varium		
Bryum angustirete		
Bryum lonchocaulon		
Dicranoweissia cirrata		
Didymodon tophaceus		
Eurhynchium stokesii		
Fissidens grandifrons		

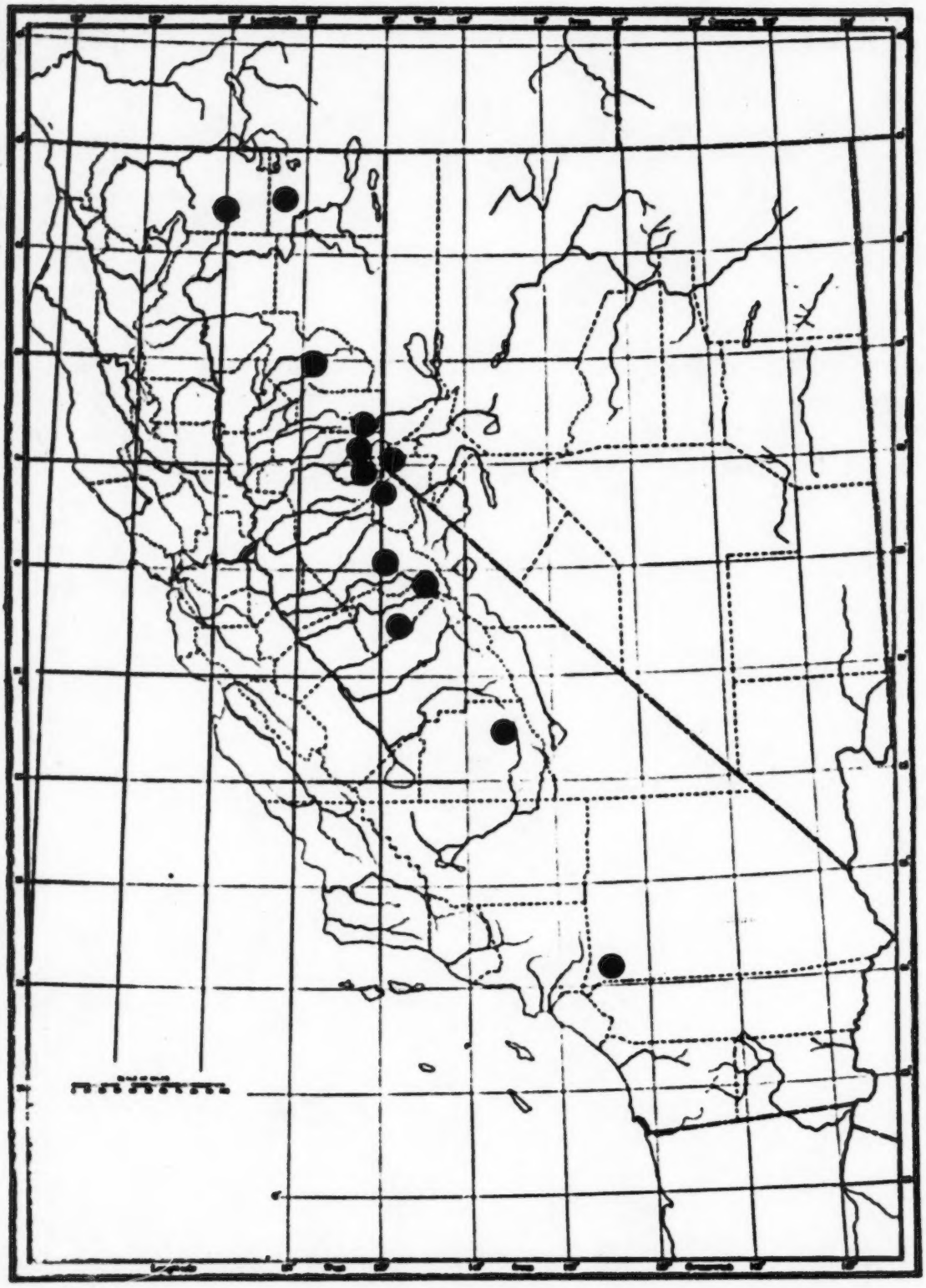


Fig. 2—Montane distribution pattern of Californian Mosses represented by known stations of *Orthotrichum laevigatum*

Species	Californian Range in Degrees North Latitude	Major Pattern of Distribution in California
Grimmia alpestris	42-32	Widespread
Hygroamblystegium tenax		
Mniobryum wahlenbergii		
Orthotrichum lyellii		
Phascum cuspidatum		

Species	Californian Range in Degrees North Latitude	Major Pattern of Distribution in California
Philonotis fontana		
Platyhypnidium riparioides		
Pohlia annotina		
Barbula convoluta		
Dichodontium pellucidum		
Dicranella heteromalla	42-36	Widespread
Orthodicranum strictum		
Sphagnum subsecundum		
Atrichum undulatum		
Dicranum fuscescens		
Dicranum scoparium		
Ditrichum ambiguum	42-37	Widespread
Mnium medium		
Pterigynandrum filiforme		
Sphagnum squarrosum		
Tortula subulata		
Hygrohypnum molle		
Hygrohypnum smithii	42-32	Montane
Orthotrichum laevigatum		
Rhaconitrium patens		
Grimmia maritima	42-39	Coastal
Plagiothecium undulatum		
Entosthodon attenuatus	40-32	Coastal
Acaulon muticum	40-36	Coastal
ASIA-NORTH AMERICAN DIVISION		
Claopodium crispifolium		
Hypnum circinale	42-37	Widespread
Mnium glabrescens		
Rhacomitrium varium		
Pogonatum contortum	42-40	Coastal
NORTH AMERICAN DIVISION TRANSCONTINENTAL ELEMENT		
Philonotis americana	42-32	Montane
ROCKY MOUNTAINS AND WESTWARD ELEMENT		
Brachythecium asperrimum		
Brachythecium petrophilum	42-32	Widespread
Fissidens limbatus		
Physcomitrium megalocarpum	42-37	Widespread
Scouleria aquatica		
ARID SOUTHWESTERN UNITED STATES AND NORTHERN MEXICAN ELEMENT		
Entosthodon bolanderi	39-32	Coastal
Crossidium desertorum	35-32	Coastal
Pottia arizonica		
Grimmia moxleyi	37-32	Desert
PACIFIC SLOPE ELEMENT		
Amphidium californicum		
Anacolia menziesii		
Bestia cristata		
Brachythecium lamprochryseum		
Bryum crassirameum		
Camptothecium amesiae		

Species	California Range in Degrees North Latitude	Major Pattern of Distribution in California
Tetraphis pellucida	42-39	Widespread
Camptothecium lutescens	42-40	Widespread
Bryum bicolor *Tortula intermedia* *Funaria muhlenbergii*	40-32	Widespread
Amphidium lapponicum *Blindia acuta* *Brachythecium collinum* *Bryum pallescens* *Desmatodon latifolius* *Desmatodon systilius* *Dicranella subulata* *Distichium inclinatum* *Encalypta rhabdocarpa* *Hygrohypnum ochraceum* *Mnium marginatum* *Oncophorus virens* *Pseudoleskea atrovirens* *Sphagnum teres* *Tortula norvegica*	42-36	Montane
Hookeria lucens	42-39	Coastal
Orthodontium gracile *Rhacomitrium canescens*	42-37	Coastal
Aloina rigida *Pottia bryoides* *Pottia starkeana*	38-32	Coastal
Tortula inermis	38-32	Desert
EUROPE-NORTH AMERICAN DIVISION		
Antitrichia californica *Aulacomnium androgynum* *Bartramia stricta* *Claopodium whippleanum* *Fabronia pusilla* *Orthotrichum tenellum* *Scleropodium cespitans* *Scleropodium tourretii*	42-32	Widespread
Bryum miniatum *Epipterygium tozeri* *Fissidens rufulus* *Grimmia montana* *Neckeradelphus menziesii* *Orthotrichum rivulare* *Tortula latifolia*	42-36	Widespread
Camptothecium arenarium *Camptothecium pinnatifidum* *Dendroalsia abietina* *Homalothecium nevadense* *Homalothecium nuttallii* *Pleuridium bolanderi* *Pseudisothecium stoloniferum*	42-32	Widespread

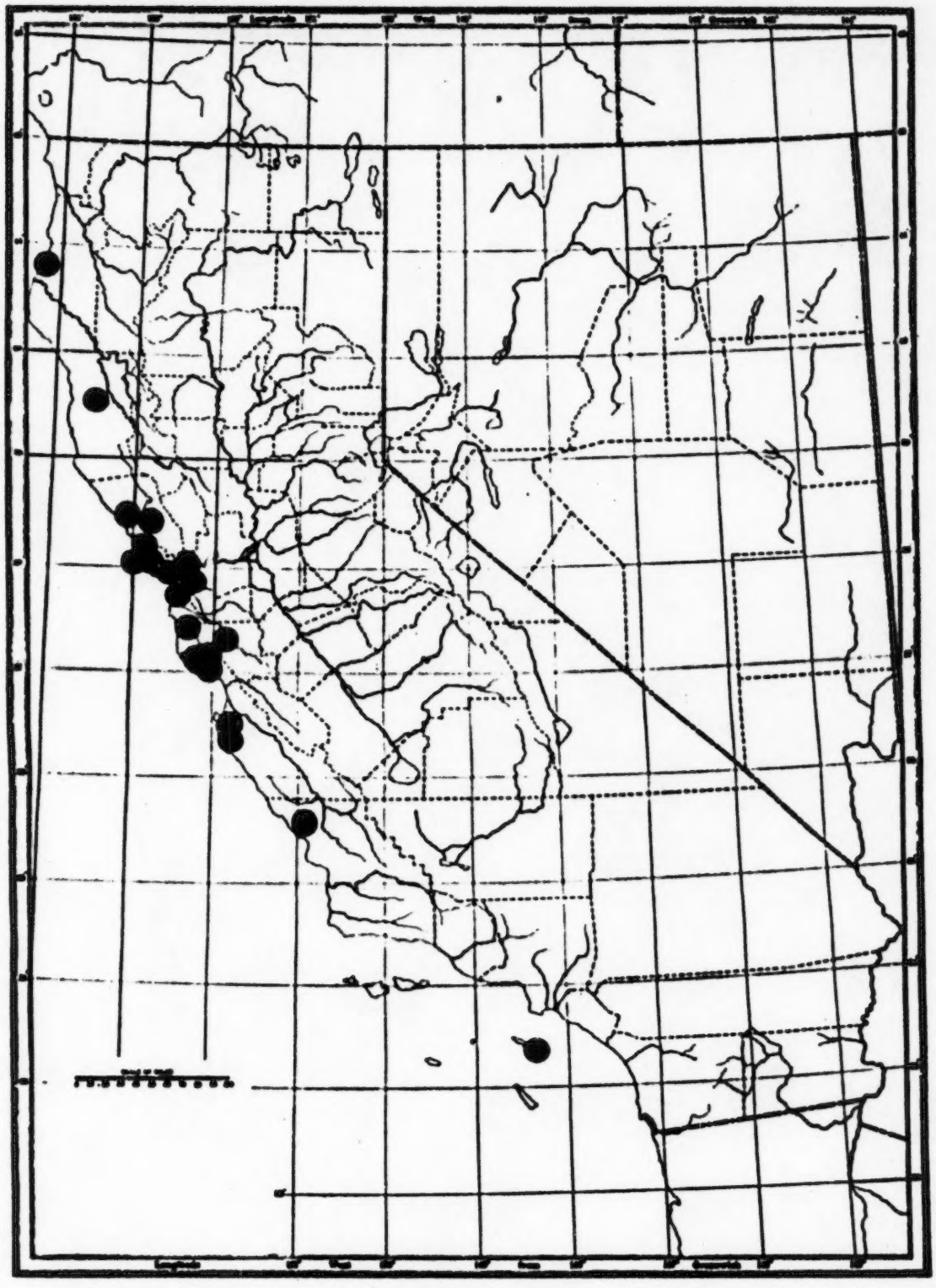


Fig. 3—Coastal distribution pattern of Californian Mosses represented by known stations of *Alsia californica*

Species	California Range in Degrees North Latitude	Major Pattern of Distribution in California
Pseudobraunia californica		
Scleropodium colpophyllum		
Scleropodium obtusifolium		
Timmiella crassinervis		
Tortula bolanderi		

Species	California Range in Degrees North Latitude	Major Pattern of Distribution in California
Ditrichum schimperi *Eurhynchium oreganum* *Leucolepis menziesii* *Mnium insigne* *Orthotrichum consimile* *Porothamnium bigelovii* *Ptychomitrium gardneri*	42-37	Widespread
Hypnum subimponenens *Mnium venustum*	42-38	Widespread
Grimmia atricha *Hygrohypnum bestii* *Polytrichadelphus lyallii* *Rhacomitrium depressum* *Roellia lucida* *Scouleria marginata*	42-36	Montane
Alsia californica	38-32	Coastal
Bestia longipes	42-34	Coastal
Bestia holzingeri *Neckera douglasii* *Pohlia longibracteata*	42-37	Coastal
Bestia occidentalis	42-38	Coastal
Heterocladium heteropteroides	42-39	Coastal
Tortula brevipes	39-32	Coastal
CALIFORNIA AND NORTHERN BAJA CALIFORNIA ELEMENT		
Brachythecium bolanderi *Camptothecium alsioides* *Orthotrichum bolanderi*	39-32	Widespread
Bruchia bolanderi *Grimmia brevirostris* *Grimmia hamulosa*	40-36	Montane
Tortula amplexa	40-35	Coastal
Scleropodium californicum	39-33	Coastal

Literature pertaining to plant geography contains many references to "oceanic" and "continental" species or groups of species (i.e. Hulten, 1937). Other phytogeographers, like Amann (1928) refer to "Arctic-Alpine" or "Arctic-Montane" groups of species. These terms have occasionally been used in a geographical sense but are essentially ecological concepts and are omitted from the geographical subdivision used here for boreal mosses. Perhaps these concepts can be integrated into the subdivision of the boreal floral elements into fractions.

DISCUSSION AND CONCLUSIONS

The major distributional patterns of the mosses in California show interesting differences from, and similarities with, the units of the various systems of classification applied to vegetational types in California. Seven systems

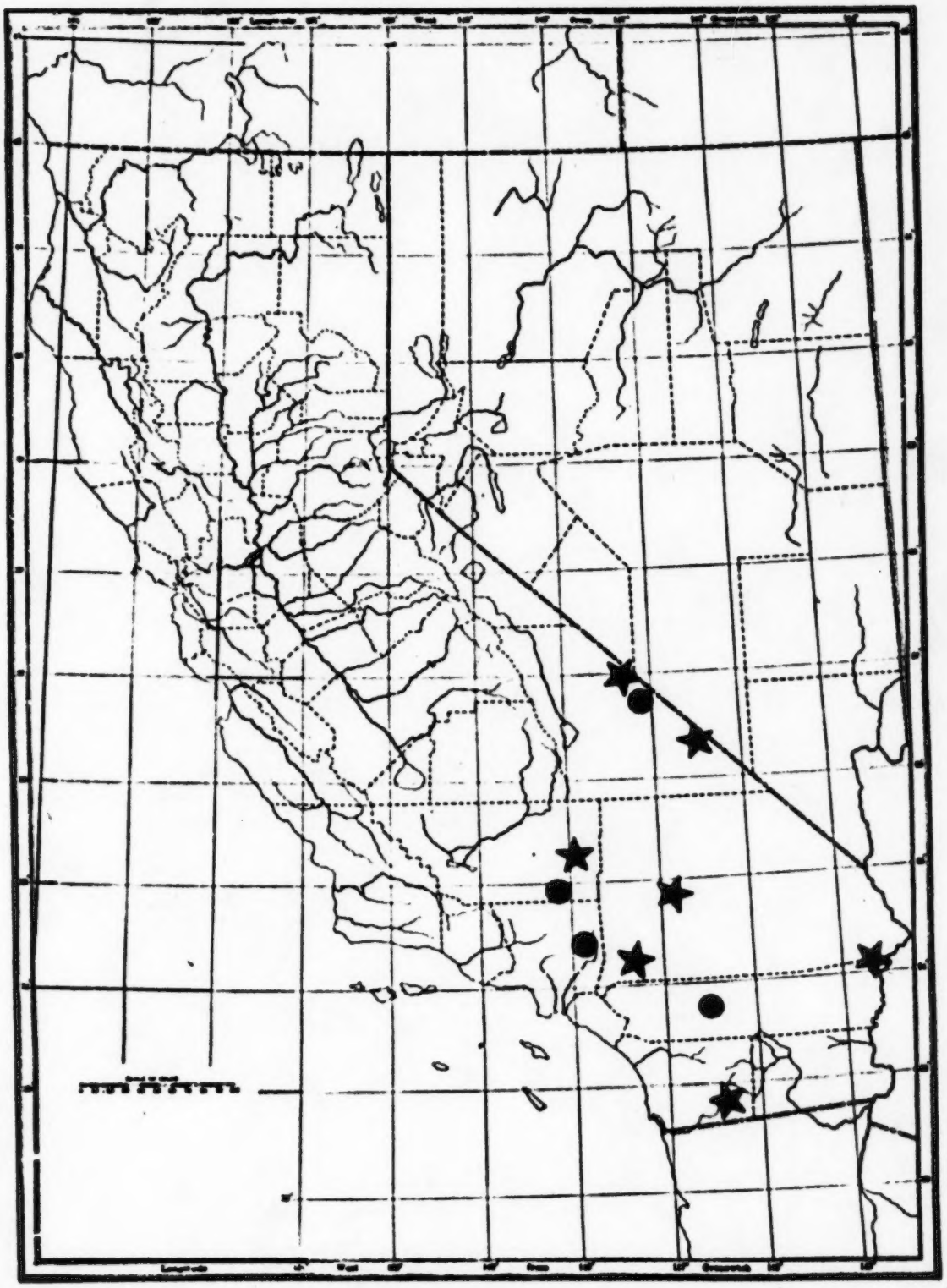


Fig. 4.—Desert distribution pattern of Californian Mosses represented by known stations of *Grimmia moxleyi* and *Tortula inermis*. The former species is represented by dots; the latter by stars.

considered in detail are those proposed by Merriam (1898), Shreve (1917), Shantz and Zon (1924), Weaver and Clements (1938), Dice (1943), Jensen (1947), and Munz and Keck (1949).

The four major patterns of moss distribution (Widespread, Montane, Coastal and Desert) uniformly agree more closely with the units proposed by Shreve (1917) than with any other mentioned above. Detailed analyses, com-

parisons, and conclusions about the remaining systems of vegetational units in California are included in my doctoral thesis (Koch, 1950c).

The region in California occupied by the Widespread groups of mosses agrees closely with an area which is a combination of the Californian parts of Shreve's "Northwestern Hygrophytic Forest," "Northern Mesophytic Evergreen Forest," and "Pacific Semi-Desert." Conversely, these mosses do not occur in the desert areas which Shreve called the "Californian Microphyll Desert" and the "Great Basin Microphyll Desert."

The Montane groups of species have distributional patterns corresponding with the Sierra Nevada segment of Shreve's "Northern Mesophytic Evergreen Forest." The stations south of the Sierra Nevada can be correlated with the disjunct segments of that vegetational area in southern California.

The three largest Coastal groups of mosses have northern or southern limits of distribution which correspond with the boundaries of certain vegetational regions described by Shreve. The line at the coast between the "Pacific Semi-Desert" and the "Northern Mesophytic Evergreen Forest" agrees with the northernmost stations of the five species in the groups "Coastal, 38-32 degrees north latitude." Six mosses in the groups "Coastal, 42-39 degrees north latitude" have southernmost known stations a few miles north of that same line. Five species in the groups "Coastal, 42-37 degrees north latitude" have their known southernmost stations in an isolated section of the Redwood forest in Santa Cruz County. This is indicated as a disjunct segment of the Northern Mesophytic Evergreen Forest by Shreve.

The known distribution of the two Desert mosses corresponds very closely with Shreve's Californian Microphyll Desert.

Three of Shreve's areas (Northwestern Hygrophytic Evergreen Forest, Northern Mesophytic Evergreen Forest, and Western Xerophytic Evergreen Forest) are largely characterized by conifers whereas the other four areas have a flora without a coniferous fraction, or whose conifers are largely limited to one region. The distribution of *Pinus jeffreyi*, as depicted by Cain (1944), closely matches the Sierra Nevada section of Shreve's Northern Mesophytic Evergreen Forest.

None of Jepson's endemic areas agrees with the range of either of the two redwoods (Shirley, 1947) but the area occupied by the Montane mosses endemic to California corresponds closely to that in which *Sequoia gigantea* is found. *Fissidens pauperculus* has been found only in localities (Koch, 1948, 1949, 1951b) where the coast redwood predominates. The restricted North American occurrence of *Orthodontium gracile* on stumps or trunks of the coast redwood is also interesting.

Perhaps the close correspondence of the patterns of distribution of Californian mosses with the units demarcated by Shreve can be linked to a common similarity in the distribution of mosses and conifers.

GEOGRAPHICAL DISTRIBUTION OF MOSSES COMPARED WITH HIGHER PLANTS

The data taken from Campbell and Wiggins (1947) for the higher plants of California have been rearranged to correspond to the divisions and elements of the boreal mosses as closely as possible. Corresponding groups are placed opposite each other in the following table for the sake of comparison.

Mosses	Percentage of Total Flora	Higher Plants	Percentage of Total Flora
Both hemispheres	24.0	Cosmopolitan	0.9
Three boreal continents	31.9	North Temperate Zone	1.2
		California, Circumpolar	1.1
Europe-North America	12.2	United States, Eurasia	1.8
Asia-North America	1.6		0.0
Transcontinental North America	0.9	California, East Asia	0.3
		Temperate North America	0.9
Rocky Mountains and Westward	2.5	California to eastern North America	4.4
		Western United States and Canada	18.3
Southwestern United States and northern Mexico	2.8	California to central Mexico	2.8
Pacific Slope	17.6	California to northern Mexico	5.1
		Pacific States	14.5
California and northern Baja California	5.3	California to Alaska	2.5
		California to Baja California	36.0
Anomalous	1.3	Miscellaneous	9.0
Totals	100.1	Totals	98.8

In spite of the large differences in percentage of the total flora in comparable groups of the mosses and higher plants, the direction of origin of similar groups is probably the same. Among the extraneous elements, the Widespread and Coastal species having their known southernmost North American stations in California or Baja California, as well as the Montane groups of species, probably entered California from the north whereas those Widespread and Coastal species having northernmost stations in California probably entered California from the south. The Desert species whose affinity is with mosses of adjacent deserts had their origin wherever late Tertiary deserts were located. The endemic mosses probably evolved since the isolation of California from the rest of North America at the close of the Cretaceous in line with the reasoning of Campbell and Wiggins (1947) that endemic Californian plants originated in their present area. Nothing definite can be said about those groups of plants known from both hemispheres or from far north and south of the state.

DISTRIBUTIONAL AREAS OF CRYPTOGAMS AND PHANEROGAMS

Percentages for four comparable groups, extracted from the tabular comparison of the geographical affinities of mosses and higher plants, are interesting:

PERCENTAGE OF TOTAL FLORA OF CALIFORNIA

	Mosses	Higher Plants
California and Baja California	5.3	36.0
North America only	29.1	84.5
Restricted to Boreal Hemispheres	74.7	97.6
Both Hemispheres	24.0	0.9

A logical generalization from these data is that in any limited area the percentage of endemic mosses is smaller than the percentage of higher plants endemic to the same area. Other groups of cryptogams having fewer endemic species than do higher plants in California are liverworts (Howe, 1896) and

lichens. On the basis of the seeming correlation between conifers and mosses in connection with Shreve's vegetational areas, conifers may belong in the same distributional category as the cryptogams noted above.

The distributional areas of the individual endemic mosses whose known stations are numerous enough to indicate a pattern, are larger than the areas of endemism outlined by Jepson (1925) for higher plants. For example, *Sclerodium californicum* and *Tortula amplexa* occupy an area almost coextensive with three of Jepson's areas (Franciscan, Lucian, and Santa Barbara Insular). *Orthotrichum bolanderi* and *Brachythecium bolanderi* occur in at least four of Jepson's areas (Low Foothill Area, Franciscan Area, Lucian Area, and Santa Barbara Insular Area). Jepson did not describe an area of endemism in the high Sierra Nevada, but the range of altitudes of known stations of the endemic Montane mosses (4,000-10,000 feet) exceeds that given by Jepson (3,000-7,000 feet) for his Tehaman Area. In view of these facts, a second generalization about the distribution of endemic plants in California may not be amiss. In any limited area, the individual distribution of endemic mosses is more widespread geographically than the distribution of higher plants endemic to the same area.

These two generalizations may be interpreted as two fundamental hypotheses relating to the geography of mosses and higher plants generally. These postulates are true for California and will serve as working hypotheses for other and larger areas.

The following ideas or theories may be pertinent to the validity of our two generalizations:

1) The belief that cryptogams have wider distributional areas than higher plants because their spores are widely distributed by air currents influenced plant geographers of the nineteenth century to disregard cryptogams almost entirely in phytogeographic analyses. With the advent of more accurate knowledge, both taxonomic and distributional, investigators particularly Christ (1910), and Herzog (1926), concluded for ferns and bryophytes respectively that the distribution of these plants, on the whole is parallel to that of seed plants. Cain (1944) stated that conclusions about the geography of the flowering plants can be extended to cryptogams and are supported by them. Further evidence similar to that compiled for Californian mosses and higher plants may necessitate certain qualifications for this generalization.

2) Herzog (1926) decided that endemism among the bryophytes is less than among the higher plants. He concluded that, "Wenn trotzdem die Moose, und unter diesen die Lebermoose noch in erhöhtem Masse, die zahlenmässig so viel weniger Endemism geliefert haben als die Angiospermen, so liegt dies meines Ertrachten an der langsameren Umbildung ihres Art materials, überhaupt was ich auf die geringeren kombinations- und Ausfallsmöglichkeiten von Merkmalen bei niederen organisierten Pflanzen zurückführen möchte."

3) Harvill (1950) suggested that the "very age of bryophytes may make the widespread distribution of some species likely." Extreme age of a taxonomic entity necessarily implies the existence of additional attributes. A species of Carboniferous age must have had a considerable range of tolerance, in the sense of Good (1947), and also must have been comparatively stable genetically, to survive intact the environmental changes which exterminated

most Carboniferous plants. Age accompanied by evolution into a different taxonomic entity retains no significance to theories based on identity.

An ancient history would make possible the distribution of a species over areas now separated by barriers if that species had access to migration routes before the barrier arose. Harvill's statement is probably true insofar as Willis' theory of "Age and Area" is applicable, but how can "Age and Area" explain the wider distribution of endemic mosses than endemic higher plants in a limited area like California, which has been continuous and also isolated since the Cretaceous?

The functional principle, causing different distribution in the same area during the same time is more likely to be something in the makeup of the two groups of plants. Herzog's idea of slower speciation, based on fewer available characteristics in the simpler organism, certainly bears consideration. A fundamental premise like Herzog's applies equally well to the percentage of endemic species and to their individual distribution.

4) Bryophyte floras have not been adequately studied, and more complete knowledge may lessen, or account for, the difference in percentage of endemism and distribution.

5) Systematists of higher plants may have split their taxonomic entities into species comparable to the subspecies of bryophytes. There is no indication that this statement is applicable to the flora of California but it seems to be a corollary of the previous idea.

6) Bryophytes, because of their small size, may be able to persist in, or invade microhabitats in which seed plants of similar ecological amplitude cannot exist because they are larger above ground and have in most cases extensive root systems below ground. The investigation of microclimates in Neotoma Valley, Ohio, by Wolfe, Wareham, and Schofield (1949), indicates that the principle of microhabitats may be of paramount importance. At any rate, the presence of microhabitats probably influences the patterns of plant distribution directly and may represent a most profitable subject of investigation in the future.

7) Bryophytes may have greater tolerances, in the sense of Good (1947), than higher plants and can grow in more varied environments.

Evidence directly applicable to these questions of the geography of mosses versus higher plants, if it has been published, has not come to my attention.

TWO EXAMPLES OF POSSIBLE FLORAL FRACTIONS AND UNITS

The present composition of the "California and Baja California Element" can hardly be considered homogeneous. More nearly correct would be its subdivision into a Sierra Nevada, Pacific Semi-Desert, and a California Coastal Element in line with the distributional patterns exhibited by the few endemic mosses about which there is adequate data. When the remaining endemic species have become sufficiently well known this more elaborate list of intraneous elements will probably be justified. Two of these groups can be tentatively interpreted as follows:

The first, "Widespread, 39-32 degrees north latitude," includes two species (*Orthotrichum bolanderi* and *Brachythecium bolanderi*) reasonably well known, whose distribution (fig. 1) corresponds to the cismontane region in California and Baja California designated the "Pacific Semi-Desert" by Shreve. The predominant vegetational type in the area is chaparral. Except for iso-

lated mountains the area is relatively uniform climatically. These mosses may represent a group comparable to the "Baja California and cismontane southern California" derivatives of Sharsmith's "Sonoran floristic element."

The second, "Montane, 40-36 degrees north latitude," (fig. 2) includes *Grimmia brevirostris* and *G. hamulosa*, each with a number of known stations, whose distributional area between 4,000 and 10,000 feet above sea level in the Sierra Nevada, agrees roughly with the region occupied by *Sequoia gigantea*. Presumably they are montane species in an ecological sense.

On the basis of similar geographical distribution, and essentially equivalent ecological requirements, each of these groups may represent a floral fraction of an intraneous element. In the absence of evidence to the contrary, and in line with the theory of Campbell and Wiggins (1947) that endemic Californian plants originated in their present area, the species in each group may be assumed to have a common migrational history and represent floral units. Each unit can most readily be designated by one of its component species.

SUMMARY

Literature on mosses in California was critically reviewed; the occurrence of 258 species in California was verified, 20 species remain doubtful, and 68 names of mosses previously reported for California were excluded. Approximately 10,000 specimens of mosses from California were examined and 43 species were added to the known flora bringing its total to 320 species for California.

The concept of floral (floristic, or phytogeographic) element, as expressed in literature dealing with plant geography is considered inadequate because groups of species resulting from its application are too heterogeneous for convenient use in discussing problems of interpretive plant geography.

Derivation of more homogeneous groups of species is proposed by the application of evidence from descriptive plant geography, descriptive ecology, and geology in three successive steps. Species are classified first according to their geography, secondly according to ecology, and finally according to geology. The basic, "floral unit" of interpretive plant geography is a group of taxonomic entities having a basically similar pattern of distribution, essentially equivalent ecological characteristics, and a common migrational history.

The known world-wide geographical affinities of the present moss flora of California were ascertained by a survey of available literature. Seventy-seven mosses (24.0%) occurring in both the northern and southern hemispheres are grouped according to an apparent correlation of climate and their known distribution in the absence of sufficient knowledge for the delineation of floral divisions. Two hundred thirty-nine mosses (74.7%) known only from the northern hemisphere are classified according to their presence on, or apparent absence from, continents. The resulting groups of species are designated "floral divisions."

The North American Division (species restricted to North America) of the Californian moss flora is subdivided into five tentative "floral elements" on the basis of similar geographical distribution of individual species. The remaining divisions cannot be subdivided because of incomplete knowledge.

Distributional patterns of mosses in California were determined by mapping known stations for each species in the flora. Four major types of distribution

in California which may result from ecological limitations of ranges are Widespread, Montane, Coastal and Desert.

Distributional patterns of Californian mosses were compared with the units of seven systems of classifying vegetational units in the state. They correspond more closely with the unit areas of Shreve (1917) than with the units of any other system considered.

Shreve's vegetational frontiers appear to correspond with the limits of distribution of certain conifers. The distribution of conifers may be closely linked with that of bryophytes; this may account for the similarity between the distributional patterns of mosses and Shreve's vegetational areas. The common antiquity of bryophytes and conifers when compared to higher plants makes this hypothesis logical but no direct evidence can be cited.

The geographical distribution of Californian mosses was compared with that of higher plants. Percentages of species in comparable groups are considerably different but the corresponding groups are believed to have had similar origins. Coastal and Widespread mosses with known southernmost stations in California or Baja California, and Montane groups of species restricted to the northern hemisphere, probably represent southern extensions of the boreal flora. Coastal and Widespread groups with northernmost stations in California are probably northern extensions of the subtropical, Mexican flora. Desert species originated wherever deserts of the late Tertiary were located.

Differences in the geographical distribution of mosses and higher plants in California were made the basis for two hypotheses relating to geography of mosses and higher plants generally. In any limited area (1) there is a smaller percentage of endemic mosses than of higher plants, and (2) endemic mosses, individually, are more widely distributed than most endemic higher plants. No direct evidence is known but seven theories or ideas are discussed and may partially explain the different distribution of mosses and higher plants of California.

The mosses endemic to California and Baja California probably represent three floral elements corresponding to the three major distributional patterns exhibited by them. An apparent correlation of the distribution of two groups of endemic mosses, vegetational areas, and climate is considered an indication of floral fractions, and possibly floral units of Californian mosses.

REFERENCES

ABRAMS, L. 1925—The origin and geographical affinities of the flora of California. Ecology 6:1-6.

AMANN, J. 1928—Bryogeographie de la Suisse. Zurich.

AXELROD, D. I. 1939—A Miocene flora from the western border of the Mohave Desert. Carnegie Inst. Wash. Publ. 516.

CAIN, S. A. 1944—Foundations of plant geography. Harper Brothers, New York and London.

CAMPBELL, D. H. AND I. L. WIGGINS 1947—The origin of the flora of California. Stanford Univ. Publ. Univ. Series, Biol. Sci. 10:1-20.

CHANEY, R. W. 1944—Pleiocene floras of California and Oregon. Carnegie Inst. Wash. Publ. 553.

CHRIST, H. 1910—Die Geographie der Farne. G. Fischer, Jena.

COOPER, W. S. 1922—The broad-sclerophyll vegetation of California. Carnegie Inst. Wash. Publ. 319.

———1926—The fundamentals of vegetational change. Ecology 7:391-413.

DICE, L. R. 1943—The biotic provinces of North America. Univ. Mich. Press, Ann Arbor.

GOOD, R. 1947—The geography of flowering plants. Longmans, Green and Co. London, New York.
GROUT, A. J. 1928-1940—Moss flora of North America north of Mexico. Vols. 1-3. Newfane, Vermont.
HARVILL, A. M., JR. 1950—Notes on the mosses of Alaska III. Some new or otherwise interesting records. Bryol. 53:16-25.
HERZOG, T. 1926—Geographie der Moose. G. Fischer, Jena.
HOWE, M. A. 1896—A comparison of the hepatic flora of California with that of the eastern United States and of Europe. Erythea 4:60.
———1898—*Hepaticae* and *Anthocerotes* of California. Mem. Torr. Bot. Club 7:1-208.
HULTEN, E. 1937—Outline of the history of Arctic and boreal biota during the Quaternary period. Stockholm.
JENSEN, H. A. 1947—A system for classifying vegetation in California. Calif. Fish and Game 33:199-266.
JEPSON, W. L. 1925—Manual of the flowering plants of California. Univ. Calif. Press, Berkeley.
KOCH, L. F. 1948—Rediscovery of *Fissidens pauperculus* Howe. Bryol. 51:30-31.
———1949a—Preliminary studies of Californian mosses I. Ibid. 52:84-89.
———1949b—The nomenclature of *Hypnum illecebrum*. Rev. Bryol. Lich. 18:176-178.
———1950a—Mosses of California: an annotated list of species. Leafl. West Bot. 6:1-40.
———1950b—Mosses of California II. *Zygodon viridissimus*. Bryol. 53:213-215.
———1950c—The distribution of Californian mosses. Thesis. University of Michigan, Ann Arbor. Microfilm publication.
———1951a—Mosses of California III. *Bryum tortifolium* and *Stroemia obtusifolia*. Bryol. 54:69-70.
———1951b—*Fissidens pauperculus* Howe and *Orthodontium gracile* Bruch and Schimper: Mosses associated with the coast redwood forest. Science 114:571-2.
———1951c—Mosses of California IV. *Fissidens milobakeri* sp. nov. Bryol. 54:204-207.
LESQUEREUX, L. 1865—On the mosses of California. Philadelphia. Preprint. (Also in Am. Phil. Soc. Trans. 13:1-24, 1869.)
LYNGE, B. 1932—A revision of the genus Rhizocarpon (RAM) Th. Fr. in Greenland. Skrifter om Svalbard og Ishavet No. 47.
MASON, H. L. 1947—Evolution of certain floristic associations in western North America. Ecol. Mon. 17:201-210.
MERRIAM, C. H. 1898—Life zones and crop zones of the United States. U. S. Dept. Agric., Div. Biol. Surv., Bull. 10.
MUNZ, P. A. AND D. D. KECK 1949—California plant communities. El Aliso 2:87-105.
RAUP, H. M. 1942—Trends in the development of geographic botany. Ann. Assoc. Am. Geogr. 32:319-354.
SHANTZ, H. L. AND R. ZON 1924—Atlas of American agriculture. The physical basis of agriculture. Natural vegetation. Govt. Printing Off., Wash., D. C.
SHARSMITH, H. K. 1945—Flora of the Mount Hamilton Range of California. Amer. Midl. Nat. 34:289-367.
SHIRLEY, J. C. 1947—The Redwoods of Coast and Sierra. Univ. Calif. Press, Berkeley and Los Angeles.
SHREVE, F. 1917—A map of the vegetation of the United States. Geogr. Rev. 3:119-125.
STEERE, W. C. 1951—*Tortula stanfordensis*. A new species from California. Bryol. 54:119-123.
WEAVER, J. E. AND F. E. CLEMENTS 1938—Plant ecology. McGraw-Hill Book Co., New York and London.
WOLFE, J. N., R. R. WAREHAM AND T. T. SCOFIELD 1949—Microclimates and macroclimates of Neotoma, a small valley in central Ohio. Ohio Biol. Surv. 8:1-267.
WULFF, E. V. 1943—An introduction to historical plant geography. Authorized translation by E. Brissenden. Chronica Botanica. Waltham, Mass.

Environment and Vegetation of Tomer's Butte in the Forest-Grassland Transition Zone of North Idaho

Johnson Parker[1]
University of Idaho, Moscow

Tomer's Butte rises about 900 feet above the surrounding valley or 3,510 feet above sea level in the transition zone between grassland and forest. It is situated four miles east of the town of Moscow in Latah County, North Idaho. Today some of the grassland is cultivated and a little of the forest cut, but in spite of this there is enough conformity to original conditions to make this a place of considerable ecological interest. Although a previous study of the area has been made by Gail (1921) it is believed that certain factors in the environment have been overemphasized in their effects on the vegetation and certain others have been neglected. In order to clarify the interactions between these various factors a study of microclimate, soils, and vegetational cover was made.

Geology

This butte is one of a series of hills which represent the beginning of the mountain complex of North Idaho as one progresses from the west to the east. The principal composition of the bed rock is quartzite and is classified in the Belt Series of Algonkian age. This is in contrast to many of the adjacent hills, such as the Palouse Range which is largely granitic. The valley, especially to the south of the butte, is basalt overlain with a deposit of Quaternary or possibly Pleistocene loess which has been eroded into dune-like hills (Fig. 4). The underlying basalt varies widely in depth but the upper surface is relatively flat and slopes only slightly downward to the southwestward (Tullis, 1944).

Evidently the quartzite of the butte was affected during Cretaceous and possibly even Tertiary times by the massive intrusion of the granitic rock which appears in the vicinity of Moscow Mountain. After many thousands of years of erosion the basalt moved into the valley in relatively recent times, probably in the Miocene period. Finally, since or even during the time of the last glacial advance aeolian material has blown in from the westward and largely covered the basalt.

It is possible that the addition of new material by the wind is still continuing. Fuller (1948:19) discusses the origin of this soil which varies in depth from a few feet to 100 feet in depth and points out that at the rate of four inches of new material per century, 75 feet of soil could accumulate in 25,000

1 The writer is indebted to W. H. Baker for identifying the flowering herbs mentioned in this paper which were collected by him on this butte and placed in the University of Idaho herbarium. We are further indebted to W. K. Ferrell, M. A. Fosberg, E. J. Larrison, Malcolm Jollie, and Walter Youngquist of the University of Idaho for helpful suggestions in certain phases of this work.

years. This time is sometimes given as the interval between the last glacial withdrawal and the present time.

On Tomer's Butte the quartzite soil is mixed in varying proportions with aeolian material, the upper slopes being largely derived from quartzite and the lower slopes being largely derived from loess. The further differentiation of the soil is largely affected by direction and angle of slope, and by the vegetation growing on it.

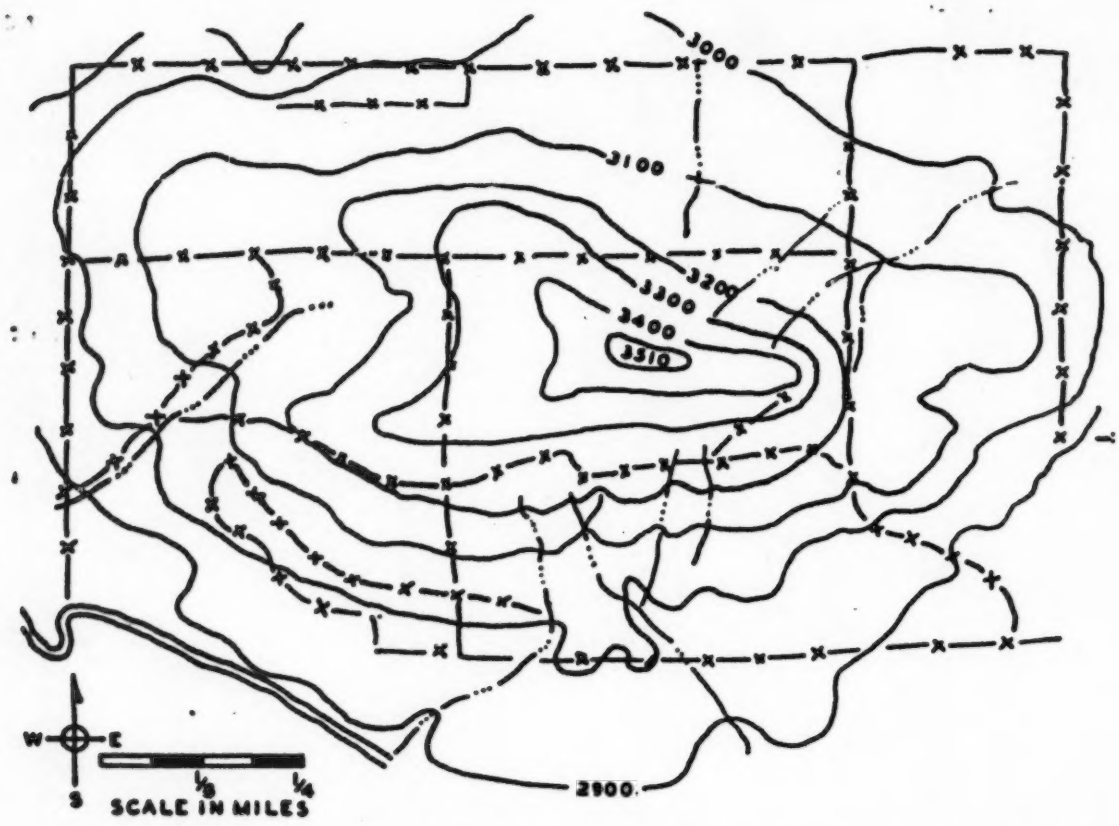


Fig. 1.—Topographic map of Tomer's Butte. Lines with crosses represent barbed-wire fences; lines with three dots at intervals are intermittent streams which are dry during most of the summer; numbers represent elevation above sea level in feet obtained from altimeter measurements.

It may be seen in figure 1 that the contour of the butte shows a fairly steep slope to the northeast, as well as a slight concavity in that direction. This may be caused by the accumulation of snow on this slope which tends to slip downwards and produces a miniature cirque. The tendency of the snow to slide downwards is shown by the bowed appearance of the trees on the upper north slopes as illustrated by Daubenmire (1947:103). The tendency for snow to accumulate on north, northeast, and east slopes is very common in the loess hills of the valley (Fig. 4) and this snowbank nivation seems to account for their concavity to the northeast. The reason for snow accumulation on this slope will be taken up under microclimate.

There is also the possibility that many of the contours of the butte are affected by the position and angle of the underlying rock. The dip of the quartzites, schists, and related rocks on nearby Paradise Ridge (3,760 ft.) is generally down to the north-northwestward at an angle of about 80 degrees.

The outcrop extends, therefore, in a more or less east and west direction and this may account for the longer east-west contours on Tomer's Butte. Whether this dip would explain the steeper north slope is a matter of conjecture.

SOILS

The soils of this area are shown in figure 2 and are about nine in number according to the survey of the Soil Conservation Service. Aside form the "Rough Stony Land" which is pastured by horses and cattle (fig. 3, above the cultivated land) there are three principal series of soils on the Butte: the Schumacher, Larkin, and Palouse.

The Schumacher series includes dark-colored lithosol-like soils with brown to yellow-brown subsoils which overlie metamorphosed quartzite and similar rocks at shallow depths. Although the soil material is mainly residual in origin, the surface soils may contain an admixture of material deposited by wind (Anon. 1949). These soils develop under grass cover with low rainfall and they are only moderately productive.

The upper layers of Schumacher silt loam, about one foot in depth, contain a large amount of organic matter and were evidently formed under a grass cover on this butte. It will be noticed by comparing figures 2 and 3 that this soil is now covered by forest. This may be explained by a later invasion of forest into the upper part of the butte. Patches of the same soil can be seen in the upper part of figure 2, and these areas were in forest about five years ago.

The area classified as Schumacher stony loam is now largely pastured and

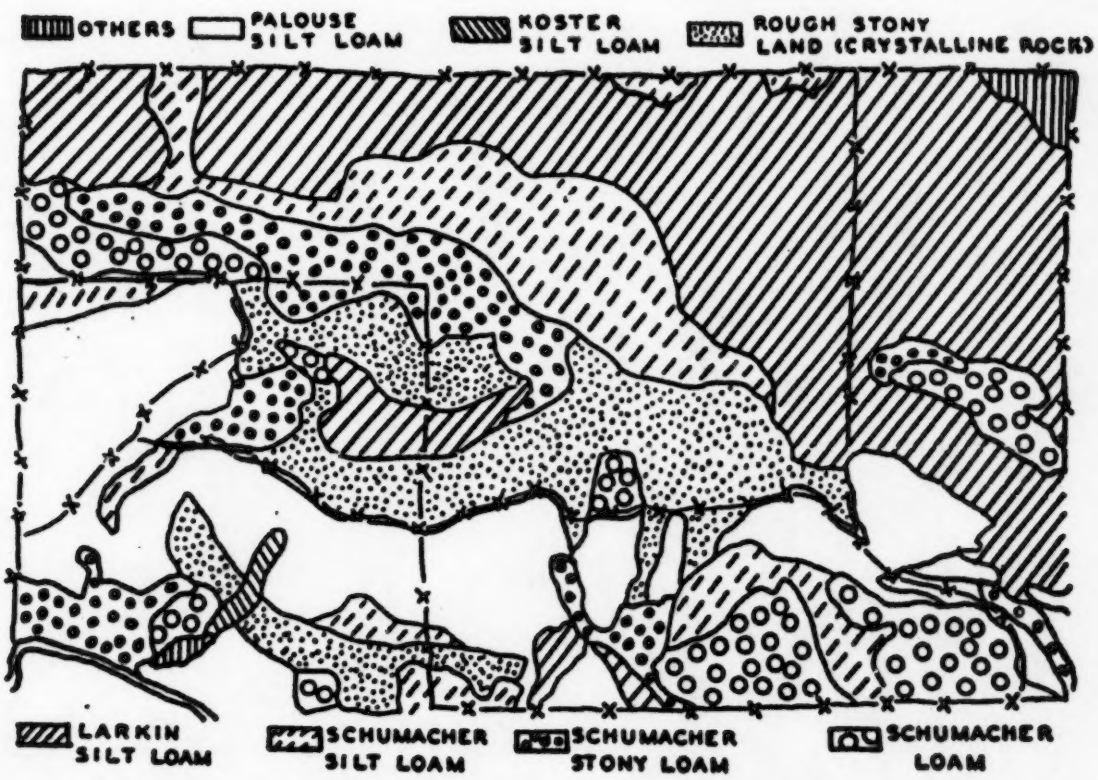


Fig. 2.—Soils map of same area as shown in figure 1 from Soil Conservation Service Survey.

its boundaries with the Rough Stony Land, also pastured, are not at all sharp. Both of these soils have been altered by the work of the pocket gopher (*Thomomys talpoides fuscus* Merriam.). The effect of these rodents is so great that the mounds which they construct are often three or four feet high and 19 feet across, and can be seen in an aerial photograph (center of fig. 3). Other theories for the origin of these mounds have been proposed, theories based largely on erosional effects, but these mounds exhibit no profile, nor are they underlain with a rock outcrop projecting slightly above the general level of the ground. The mound soil appears to be well mixed to a depth of about 3 feet containing some gravel and a considerable amount of organic matter, both characteristic of the shallow topsoil of the area. New tailings of the gophers are occasionally found on the mounds and the general appearance of the hummocks is very similar to those found in many other parts of the western United States which are caused by pocket gophers (Larrison, 1942).

The Larkin series is often formed over basalt under coniferous timber and much of the lower north slope of the butte is classified in this series. The series includes brownish-gray or light brown soils with yellowish colored mottled, heavy-textured subsoils. However, this underlying rock of this butte is not basalt and the surface soil has a large amount of organic matter so that it seems to resemble to some extent the Schumacher silt loam found higher up. It was apparently more convenient to classify it in the Larkin series because of its close resemblance to Larkin soils found elsewhere.

The lower south slopes are classified as Palouse silt loam, but there is some tendency toward Schumacher silt loam in the upper slopes. The typi-

Fig. 3.—Aerial photograph of Tomer's Butte on same scale as that shown in figures 1 and 2, courtesy of Soil Conservation Service.

cal Palouse silt loam has a surface layer of silt loam high in organic residue, although on this butte cultivation has reduced this organic matter and surface erosion by wind and water have reduced the entire layer in thickness. Rills and small gulleys are very common in late winter on this soil and very little is done to retard erosion. The top soil, normally more than 12 inches deep, is underlain with 2-24 inches of light yellowish brown compact clay loam or silty clay loam. This continues to 40 inches depth where a layer of dull rich brown or tawny colored compact harsh-feeling silty clay loam is found. On the lower slopes of Tomer's Butte there is some mottling in the lowest horizon on this soil.

In the zone of Rough Stony Land just bordering on the Palouse silt loam on the south slope there has been a soil slide about 20 meters wide (Fig. 5). There is evidence of an older soil slide, possibly 10 years old, but none older than this. It is possible that the abnormal moisture content of the subsoil resulting from the heavy snows of 1948-1949 and 1949-1950 combined with the effects of overgrazing to result in the soil separating along crescentic lines and sliding two or three meters, and sometimes more, down slope.

TABLE 1.—Soil constants and moisture content in late spring expressed as a percentage of soil dry weight on Tomer's Butte.

	Horizon	Moisture equivalent	Xylene equivalent	Moisture May 30, '50	Moisture May 30, '51	Organic matter	Wilting Point
N. slope Larkin	A	41.7	15.7		28.8	16.0	12.9
silt loam, 3,050 ft.	B	28.8	9.3		29.8	5.1	8.8
N.E. slope Larkin	A	38.5	15.8		29.9	12.8	
silt loam, 3,200 ft.	B	27.4	8.8		26.5	5.4	
N. slope Schumacher	A	31.6	17.2	38.3	39.4	10.8	16.7
silt loam, 3,200 ft.	B	35.5	20.0	36.0	24.5	8.3	20.0
N. slope Schumacher	A	32.5	15.9	44.0	39.3		
silt loam, 3,350 ft.	B	30.5	15.2	56.3	24.5		
N. slope Schumacher	A	29.0	14.2		39.3		
silt loam, 3,450 ft.	B	30.0	14.0		44.0		
S. slope Rough	A	26.8	11.8	11.2	10.0	9.5	10.5
stony land, 3,400 ft.	B	26.6	10.7	16.5	14.6	6.4	10.2
S. slope Palouse	A	26.8	10.5	7.7	9.2	6.3	9.9
silt loam, 3,100 ft.	B	27.5	7.6	17.5	20.3	3.5	10.7
Near Moscow Palouse	A	23.1	8.9			5.7	
silt loam, 2,700 ft.	B	23.2	7.1			2.7	

Looking at the soils of the butte as a whole, the water holding capacity, indicated by the moisture equivalents, are higher on the north slopes (Table 1). Xylene equivalents are also higher which indicates that there is more non-imbibitional water available on north slopes. Imbibitional water values, which are obtained by subtracting M.E.—X.E. are not appreciably different on the average on the two slopes. Organic matter is generally higher in both the A and B horizons on north slopes.

Fig. 4.—Snow cornices in Palouse hills, looking south from Tomer's Butte, April 1, 1951. The valley of the Clearwater lies in the distance and Paradise Ridge is nearby at the right.

South slope soils are rather rocky and shallow near the top, becoming quite deep, at least over six feet, near the lower slopes. North slope soils are about the same depth as the corresponding south slope soils for elevations of about 3,300 feet but are higher in organic matter.

MICROCLIMATE

Most of the precipitation in this region falls during the late autumn, winter, and early spring so that the vegetation is dependent on moisture stored in the soil for most of its growth. The characteristic dry clear days of summer cause certain distinct microclimatic differences to appear on this butte, although these differences are evident during the winter to some extent as well.

The adjacent Moscow Mountain, lying some seven miles to the north is high enough to affect the total precipitation that falls on its slopes. In other words, there is more precipitation at high elevations than at low ones. Tomer's Butte, however, has little effect in this respect. Sometimes snow may be seen on the butte when there is only rain in the valley, but it is questionable whether the precipitation is much higher on the butte than in the valley. Rain gauges set on the butte showed little difference between the upper south slopes and the station kept at Moscow by Dr. K. H. W. Klages during the spring of 1950. Rain gauges on the north slope showed consistently less rain than on the south slopes for the months of April and May, but this is probably caused by the filtering effect of the trees, even though the gauges were located in open areas in the woods.

A cloud phenomenon which may affect the moisture content of plants on the top of the butte is one which involves the east wind drift of moist air from the Clearwater Valley. As this air drifts over the butte it may condense as shown in figure 6. It is doubtful, however, if this fairly common phenomenon has much effect on the plants since it usually occurs during the dormant season. Besides this, the mosses and other plants occurring on the top of the

butte are more characteristic of dry rocky ridges than high moist places.

The fact is generally accepted that the greater insolation on south than on north slopes in the region of North Idaho, even as high as the subalpine forests, results in a drying of such areas. This evidently results from higher soil evaporation and higher transpiration with a consequent drying of soil and vegetation.

In winter the sun is comparatively low over the horizon at noon so that insolation is very much lower on north slopes than on south, and snow melt is sometimes more rapid on south slopes. Also the occurrence of *Pinus ponderosa* Dougl. in fairly dense stands on north slopes tends to delay snow melt even more than it would be without the cover. In fact snow may persist on the north slope until the *Balsamorhiza* aspect is prominent on the south slope toward the end of April. In early June the sun is nearly overhead at noon, but insolation is still somewhat stronger on south slopes. By July the sun is again lower in the sky at noon and insolation is more contrastive on the two slopes.

The snow bank formed in winter probably results from a combination of lack of insolation and wind eddying. The wind may be initially east during a winter storm then swings to the south and finally into the west. During this time wind velocities generally increase. East-facing slopes have the highest immediate drift accumulation, although northeast slopes are often well covered with deep drifts. The higher insolation on east slopes than north seems to favor the accumulation of snow on northeast slopes as indicated in figure 4 in the valley, as well as on the butte. The snow cornice may have produced much of the concavity and possibly the steeper angle of contours on the north side of the butte. The topographic condition, in turn, affects

Fig. 5.—South slope of Tomer's Butte at upper edge of Palouse silt loam showing soil slip. Ditches are about five feet deep.

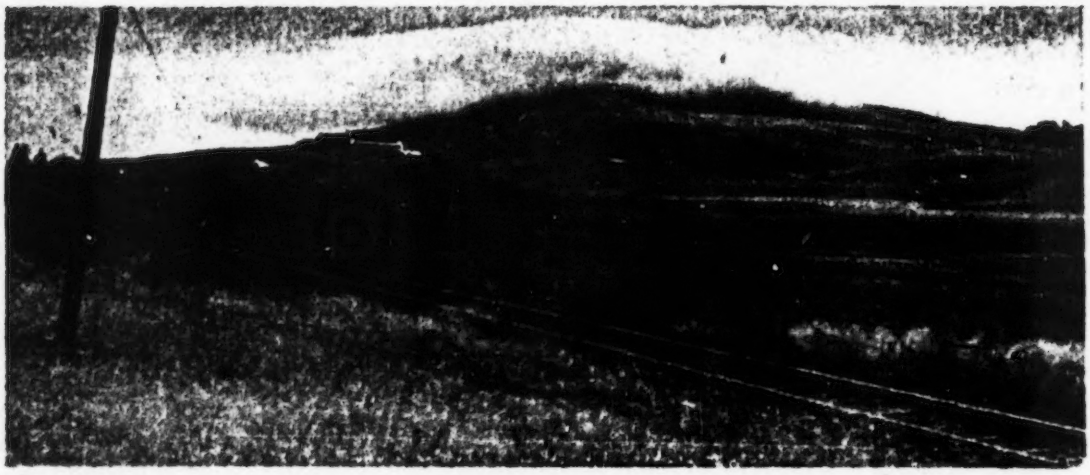


Fig. 6.—Convection fog over Tomer's Butte formed on a light east wind on an early December morning. Wind direction above the fog is light westerly.

the vegetation and therefore the ecotone between forest and forest-grassland.

It is commonly supposed that the air over north slopes is much cooler and moister than on the south slopes at a height of about three feet over the ground. This is true to only a very small extent on this butte at any time of year. Air temperature measured three feet over the ground was found to be seldom more than one or two degrees F. different on the north and south slopes provided that the thermometers employed were properly sheltered and ventilated. Average temperatures at 2:30 P.M. for the months of April and May 1950 were 56° on north slopes and 57° on south slopes.

Thermograph records of Gail (1921) show curves that are characteristic of recordings made with the elements exposed to direct insolation and which show much higher noon readings on south slopes than on north. In such a case the elements are recording their own temperature and not that of the air. In the spring of 1950 thermographs standardized against one another in a single shelter were placed on the north and south slopes of the butte and results are shown in figure 7. In this case the elements were covered with leaves which allowed some ventilation but prevented direct insolation from reaching the elements. It was found that a slight greenhouse effect is produced by such a cover, but not as much as if a cover of white paper is used which reduces ventilation.

Humidity also, in spite of the forest cover, was only slightly higher on north slopes than on south. Average values for April and May of 1950 showed 57 per cent relative humidity on north slopes and 56 on south. This is in contrast to Gail's data which shows as much as 30 per cent difference on southwest and northeast slopes. Some of this difference between our results may be explained by the fact that most of his readings were made during the summer whereas the present writer's were made in the spring. However, it is essential that both bulbs of the psychrometer be protected from the sun during a reading, a factor easily overlooked since shade is rare on south slopes and common on north.

The failure of average temperatures three feet over the ground to decrease at the usual rate of 1°C. for each 100 meters rise in elevation suggests that

the "skin of air" effect described by Geiger (1950:243) in Bavaria occurs commonly on Tomer's Butte. In such a case the isotherms tend to follow up the slopes instead of lying parallel to the valley surface.

Soil temperatures at a depth of three inches show considerable differences between open south and forested north slopes. In fair days in spring temperatures may be 45°F. at this level on north slopes and 65°F. on south slopes. On south slopes temperatures vary about 10°F. between surface soils under trees and in open grassland. It is therefore difficult to generalize on north and south slopes concerning surface soil temperature, but soil temperatures are usually higher on south slopes under cover than on north slopes under cover.

As a result of high soil temperature the vapor pressure of the soil water is also high so that the vapor pressure gradient to the air is steep. This results in a high evaporation which is not necessarily reflected in the results obtained from a white atmometer bulb standing 8 inches over the ground. Results of Weaver (1914) with atmometers on nearby Kamiak Butte are probably more representative of plant transpiration than soil evaporation but

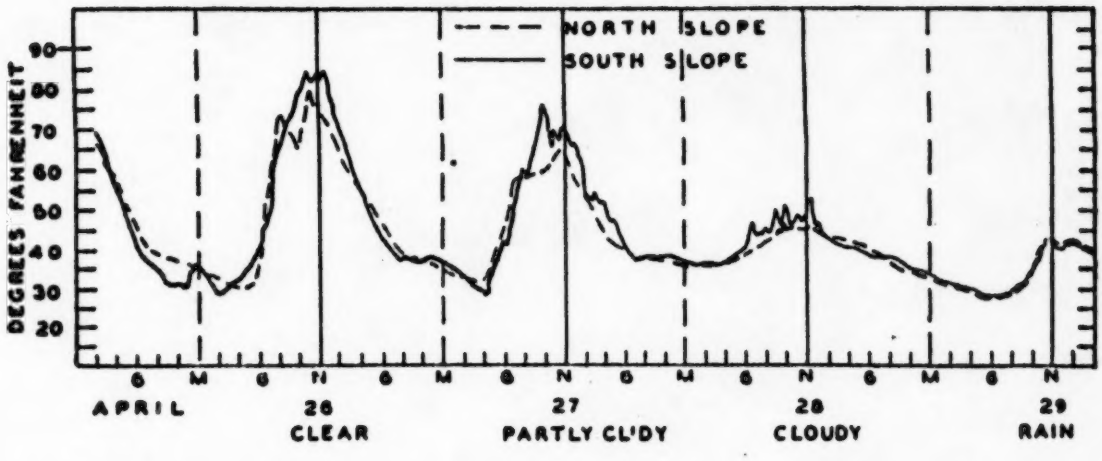


Fig. 7.—Thermograph recordings at 2,800 feet elevation on north and south slopes of Tomer's Butte, under shelter four inches above ground.

the former factor is more important in reducing soil moisture. It is now known that increased soil temperature within certain limits results in more rapid transpiration (Kramer, 1949:227), a fact generally overlooked by most ecologists. Therefore high soil temperature affects transpiration as well as evaporation from the soil itself, the two factors together having the effect of reducing soil moisture relatively rapidly. Weaver (1914) not only showed that evaporation from atmometers was considerably greater on prairie-covered southwest slopes than forested northeast slopes but also that when prairie grasses covered both northeast and southwest slopes, evaporation was much higher on southwest slopes. This work was done in vicinity of Pullman, Washington, only a few miles to the west of Tomer's Butte.

Moisture data shown in Table 1 indicates that soil moisture is above the moisture equivalent on the north slopes but well below it on south slopes at depths of four and 24 inches by the end of May. This supports the conclu-

sions of Gail (1921) who found that soil moisture approached the wilting coefficient, determined from the moisture equivalent, more rapidly on south than on north slopes of this butte. Weaver (1914) found this to be true on Kamiak Butte, as well.

Wind velocities are quite variable on different slopes, but in general this factor is often overemphasized in most considerations of environmental effects on vegetation of this region. Wind velocity measurements during April and May of 1950 showed an average of 2.2 m.p.h. on south slopes at 3,200 ft. elevation and 1.4 m.p.h. on north slopes at 3,300 ft. elevation. Gail (1921) on the other hand, reported 19 times as much wind on southwest facing slopes as on northeast. However, it is not clear whether his results were obtained on Paradise Ridge (3,760 ft.) or on Tomer's Butte (3,510 ft.). Weaver (1914) found about three times as much wind on southwest slopes of a ridge near Pullman as on northeast slopes. Both of these slopes were in prairie. Since southwest slopes are more exposed to the prevailing westerly winds than south slopes it is to be expected that there would be some difference between southwest and south slopes.

It is commonly known that forest vegetation greatly reduces wind velocity, the less the wind velocity the greater it is reduced by trees (Geiger, 1950:337). Since the north slope is well wooded and the south slope only sparsely, it is to be expected that much of the air speed reduction on the north slope is to be accounted for by the forest. Also the concavity of the north slope favors sheltering from prevailing westerlies.

The wind effect on vegetation can by no means be entirely discounted. Whereas we know that an increase of wind velocity from four to ten miles an hour results in only slightly increased transpiration (Meyer and Anderson, 1939:201), there is evidence on west slopes especially, that shrubs are strongly influenced in their shape by the wind. Also many of the tops of trees are broken and forked when they grow near the summit of the butte and shrubs like snowberry cling more to the eastern sides of gopher mounds than to northern sides. It is possible that the effect of shallow soil on the west slope combines with the direct effect of high winds to cause the bald effect. A similar bare area, covered largely with grasses, may be noticed on the west slope of Paradise Ridge.

In spite of this evidence to support the argument for the effect of wind, it is apparent that the forest-grassland ecotone runs generally in an east-west direction, following contour lines to some extent. This fact points to the importance of insolation and only secondarily to wind in affecting the distribution of forest trees and certain other plants.

VEGETATION AND FLORA

The aerial photograph (Fig. 3) gives a general idea of the forest and grassland distribution. By 1950 the forest was partly selectively cut and one large patch on the lower north slope, not shown in figure 3, was entirely cut and turned over to cultivation in 1949. This is in contrast to the south slope which has a few scattered pines interspersed with shrubs, grasses, and other herbs.

The north slope is still fairly well forested with ponderosa pine, in spite

of some cutting and recent fire. The understory is largely ninebark (*Physocarpus pauciflorus* T. & G.), snowberry (*Symphoricarpos rivularia* Suksd.), serviceberry (*Amelanchier florida* Lindl.), some willow (*Salix* spp.) and a few aspens (*Populus tremuloides* Michx.). A spring aspect of *Erythronium grandiflorum* Pursh. occurs from about April 25th to the 8th of May underneath both shrubs and trees on the north slope. This gives way to a rather sparse aspect of *Arenaria macrophylla* Hook. and some *Viola adunca* Smith, which remain in flower until about May 25th. *Amelanchier* begins to flower about May 13th and remains flowering until May 25th. All the dates given are for the spring of 1951. A number of other flowers appear on the north slope, among them *Arnica cordifolia* Hook. and *Thalictrum occidentale* Gray, which flower from the middle of May to about its end. By the end of May ninebark and buckbrush (*Ceanothus sanguineus* Pursh.) are the most prominent flowering shrubs on the north slope.

A few scattered pines occur on the south slope near the top so that the area resembles a savannah such as that illustrated by Oosting (1948:253). These scattered pines are characteristically scrubby, at best 30 to 40 feet tall and with frequently forked trunks. Site quality was found to be about V, or relatively poor, according to the chart given by Meyer (1934). However, these trees are not the type which Meyer recommends for measurement, being rather young and widely spaced. It is therefore possible that the site for this species may be better than indicated by the measurements. Trees growing in a fairly dense stand near a stream at the bottom of the south slope and picked to fit Dunning's ponderosa pine class 3 showed a site quality of III on the average.

Trees on the north slope are between about 60 and 110 feet tall decreasing in height for a given age as one progresses from the bottom to the top of the slope. Site index for trees around 100 years old in Dunning's class 3 proved to be site III near the bottom of the Schumacher silt loam area on the north slope to site IV at the top of the north slope.

Comparing Tomer's Butte with nearby Paradise Ridge or the more distant Kamiak Butte, one notices the common occurrence of Douglas fir on north facing slopes. This suggests that the north side of Tomer's Butte is a potential Douglas fir site and this idea is given support by the occurrence of Douglas firs on the northeast slope on Larkin silt loam.

The fact that many of the south slope trees are only about 40 years old whereas the north slope trees are over 100 years old in many cases indicates, as Weaver (1914) suggested on nearby Viola Ridge, that the pine is invading the grassland of the south slope. Whether this is caused by the lessened incidence of fire since the advent of farming or by a tendency for the climate to become wetter is a matter of speculation.

Pine reproduction is quite common on north slopes, but there is none on south slopes even after the unusually moist years of 1948-1949 and 1949-1950. The open-grown trees of the south slope produce a large seed crop each year and the cones carpet the ground under the trees, but no seeds or seedlings may be found. Burrows of meadow mice (*Microtus pennsylvanicus modestus* Baird) are fairly common on the lower south slopes in pasture land and together with other mice and rodents such as the red squirrel (*Tamiasciurus*

hudsonicus richardsonii Bachman) which are confined more to the areas with some tree cover, probably account for practically all the pine seed that escapes the ravages of climate and insects.

A pair of red-tailed hawks (*Buteo pamaicensis calurus* Cassin) nest near the top of the butte and these predators along with weasels, owls, and an occasional coyote do much to keep the rodent population in check. Unfortunately many of these animals are assiduously pursued and shot by farmers and others in the area.

It seems probable that if there were a good seed year together with a poor rodent year that enough seed might be produced for establishment. However, the south slope soils dry out so rapidly during the early summer that such establishment is greatly endangered.

The south slopes show a remarkable array of flowering herbs, grasses, and shrubs in the spring and most of the herbs are also remarkable for their failure to occur on the corresponding north slopes. The uncultivated area of the lower south slope shows an early aspect dominated by *Sisyrinchium douglasii* Dietr. together with many other flowering herbs such as *Collinsia parviflora* Dougl., *Draba verna* L., *Fritillaria pudica* (Pursh.) Spreng., *Lithophragma bulbiferum* Rydb., *Microsteris gracilis* (Dougl.) Greene, *Montia linearis* (Dougl.) Greene, *Ranunculus glaberrimus* Hook., *Stellaria media* (L.) Vill., and a single individual of *Populus tremuloides* Michx. By the end of April *Balsamorhiza sagittata* (Pursh) Nutt. is the most prominent herb although the previously mentioned plants are still largely in flower with the exception of *Sisyrinchium, Ranunculus,* and *Populus.* The new flowering plants towards the end of April include *Arenaria macrophylla* Hook., *Berberis repens* Lindl., *Claytonia lanceolata* Pursh., *Clematis hirsutissima* Pursh., *Delphinium nelsonii* Greene, *Dodecatheon pauciflorum* (Dur.) Greene, *Erythronium grandiflorum* Pursh., *Holosteum umbellatum* L., *Hydrophyllum capitatum* Dougl., *Leptotaenia dissecta* var. *multifida* (Nutt.) Jeps., *Lithophragma parviflorum* (Hook.) Nutt., *Lithospermum ruderale* Dougl., *Microsteris humilis* (Dougl) Greene, *Mertensia longiflora* Greene, *Montia dichotoma* (Nutt.) How., *M. perfoliata* (Donn.) How., *Saxifraga columbiana* Piper, and *Stellaria nitens* Nutt.[2]

By the middle of May most of these plants have gone to seed but the *Balsamorhiza* aspect is most prominent on the lower south slope and the *Leptotaenia* aspect is extremely prominent on much of the upper south slope. It is possible that grazing favors the *Leptotaenia* over *Balsamorhiza* in the upper pasture. As much as 50% of the cover is *Leptotaenia* in some parts of the upper south slope. At the same time *Geranium viscosissimum* F. & M., and *Brodiaea douglasii* Watts are also common and many of the grasses are beginning to flower at this time such as *Poa bulbosa* L., *Poa sandbergii* Vas., and *Bromus tectorum* L. *Geranium* and *Brodiaea* form a conspicuous part of the aspect on the south slopes by the end of May but *Wyethia amplexicaulis* Nutt. with another sunflower: *Helianthella douglasii* T. & G. are most prominent by June 4th. A number of other plants flower later in the season but are not prominent in producing an aspect appearance.

---

2 A more nearly complete list will be published by W. H. Baker.

Snowberry is very common on the south slopes and suggests that the area could support much more pine than it does. The leaves of this shrub begin to appear with the earliest flowers and are well in leaf by the time the pine buds are elongating about the middle of May. Pines on the north slopes were observed to have about the same amount of bud elongation as those on the south slopes, while the shrubs were delayed about a week in leafing out on the north slopes. Flowers such as *Erythronium* were as much as two weeks delayed in time of flowering on the north slopes as compared to the south slopes.

The top of the butte which is largely open, has a somewhat different group of herbs, starting as early as mid-March with an aspect of buttercup (*Ranunculus glaberrimus* Hook.). This is followed and accompanied by April 7th by *Antenaria dimorpha* (Nutt.) T. & G., *Claytonia lanceolata* Pursh., *Draba verna* L., *Fritillaria pudica* (Pursh.) Spreng., and *Lithofragma bulbiferum* Rydb. which remain in flower at least until the end of April. At this time the following have appeared: *Carex greyeri* Boott, *Castilleja angustifolia hispida* Fern., *C. lutea* Hel., *Collinsia parviflora* Dougl., *Cystopteris fragillis* (L.) Bernh., *Dodecatheon pauciflorum* (Dur.) Greene, *Erythronium grandiflorum* Pursh., *Holosteum umbellatum* L., *Lomatium triternatum* (Pursh.) C. & R., *Mertensia longiflora* Greene, *Montia dichotoma* (Nutt.) How., *Oregonia linearifolia* and *Sisyrinchium douglasii* Dietr. By mid-May most of these flowers have passed and *Brodiaea* and *Geranium* have become fairly common. By the end of May the only flowers of any abundance are *Sedum douglasii*, a succulent, and *Achillea millifolium* L. whose stalks remain standing for many months afterwards.

SUMMARY AND CONCLUSIONS

A study of the soils and microclimate on Tomer's Butte in the grassland-forest transition area of North Idaho shows certain differences on different slopes which have definite effects on the vegetational distribution. The greater insolation on south slopes is the most important factor in affecting vegetation, largely through its effect on soil temperature, soil moisture, and transpiration. Higher wind velocities on south slopes favor evaporation and transpiration but this is probably not as important as has been supposed. Wind velocity, however, seems to play an important role in affecting vegetation on west slopes and upper south slopes. Air temperature and humidity three feet over the ground are not as different as has been supposed on the two slopes.

Physical properties of the soil are not radically different on the two slopes, the south slopes having a moisture equivalent in the B horizon of only 4 per cent lower than on the north slopes. Wilting points determined with sunflowers show about 4 per cent difference on the two slopes.

The vegetation of the north slope is largely ponderosa pine, but judging by the plant indicators and certain other factors it is a potential Douglas fir site. The south slope for similar reasons, is probably a ponderosa pine site, but reproduction is retarded by the droughty soils and probably also by a high rodent population.

Shrubs such as snowberry are found on both north and south slopes, while others such as ninebark are confined largely to north slopes. Herbs, on the other hand, seem to reflect the microclimate immediately over the ground which is quite different on the two slopes. The few herbs that appear on the north slopes may occur on the south slopes in a few cases but the total number of herbs on north slopes is small compared to those of the south.

REFERENCES

ANON. 1949—Soils of Latah County. Mimeographed. Bu. Plant Industry, Soils, and Ag. Eng. Div. Soil Surv. U.S.D.A.

DAUBENMIRE, R. F. 1947—Plants and environment. Wiley, N. Y. 424 pp.

FULLER, G. W. 1948—A history of the Pacific Northwest with special emphasis on the Inland Empire. Knopf, N. Y. 383 pp.

GAIL, F. W. 1921—Factors controlling the distribution of Douglas fir in semi-arid regions of the northwest. Ecology 2:281-291.

GEIGER, R. G. 1950—The climate near the ground. Trans. from the German by M. N. Stewart and others. Harvard Univ. Press, Cambridge, 482 pp.

KRAMER, P. J. 1949—Plant and soil water relationships. McGraw-Hill, N. Y. 347 pp.

LARRISON, E. J. 1942—Pocket gophers and ecological succession in the Wenas region of Washington. Murrelet 23:34-41.

MEYER, B. S. AND D. B. ANDERSON 1939—Plant physiology. Van Nostrand, N. Y. 696 pp.

MEYER, W. H. 1934—Growth in selectively cut ponderosa pine forests of the Pacific Northwest. Tech. Bull. 407. U.S.D.A. Wash. D. C.

OOSTING, H. J. 1948—The study of plant communities. Freeman, San Francisco, 389 pp.

TULLIS, E. L. 1944—Contributions to the geology of Latah County, Idaho. Bull. Geol. Soc. Amer. 55:131-161.

WEAVER, J. E. 1914—Evaporation and plant succession in southeastern Washington and adjacent Idaho. Plant World 17:273-294.

Some Petrified Wood from the Specimen Ridge Area of Yellowstone National Park

Arthur F. Beyer
Midwestern University, Wichita Falls, Texas

In Yellowstone National Park practically all exposed rock formations are igneous or metamorphic consisting mostly of ash, obsidian and basalt. The central sector is made up of plateau country which though 7,000 to 8,500 feet above sea level, is nearly completely surrounded by mountain ranges rising 2,000 to 4,000 feet above it. The lava masses of Specimen Ridge in the Lamar River region are evidences of their volcanic origin and are considered by geologists to have been ejected from ancestral Mount Washburn during the early part of the Miocene or late Eocene.

Specimen Ridge cliffs which outcrop 2,000 feet above the plateau extend for 20 miles along the Lamar River and include strata wihch contain some of the most remarkable petrified trees in the park. Many superposed layers of upright petrified trunks (not less than 15 according to Knowlton [1899]) appear to indicate that in past geologic time a succession of forests flourished only to be repeatedly covered with volcanic ash and lava.

The great wealth of extinct plants of the Lamar River region must have astonished the early explorers and though reference to the area is first made by the early naturalist, W. H. Holmes (Hayden, 1873), no extended studies of the fossilized wood were made before 1899, when Professor Knowlton published his monograph *The Fossil Flora of Yellowstone National Park.*

Fossil wood specimens which Knowlton collected from the Specimen Ridge area of the park form the main body of material for anatomical reports in his monograph (1899). However, he collected plant fossils at sites other than Specimen Ridge, some of which he later investigated.

Conard (1933) discussed *Pityoxylon amethystinum* Knowlton, and, in the same year, Read investigated some fossil woods of Specimen Ridge and described those which he identified as *Pinus baumani* Read, *Pinus fallax* (Felix) Read, *Cupressinoxylon lamarense* Read, and *Sequoia magnifica* Knowlton.

In 1939, Andrews reported on anatomical details of several collections of fossil wood from Yellowstone National Park with particular reference to the fossil forest of the north-west corner of the park known as the Gallatin region. Geologically, this area is similar to Specimen Ridge. Andrews redescribed *Sequoia magnifica* Knowlton, *Cupressinoxylon lamarense* Read and *Pityoxylon* spp.

The present paper deals with a large number of pieces of petrified wood collected in Yellowstone National Park in 1941,[1] with the permission of the proper authorities. This material is retained as part of the paleobotanical collections of the University of Cincinnati (CINC).[2]

---

1 The material was collected by Dr. J. H. Hoskins, University of Cincinnati, Dr. Th. K. Just, Chicago Museum of Natural History, Dr. A. T. Cross, West Virginia Geological Survey and West Virginia University and Dr. A. H. Blickle, the Ohio University.

2 The collection (specimens and slides) include the following numbers: B-641 to B-824a.